US Army Corps
of Engineers
Waterways Experiment
Station

Wetlands Research Program Technical Report WRP-RE-10

Mitigated Wetland Restoration: Environmental Effects at Green Bottom Wildlife Management Area, West Virginia

by Dan K. Evans, Hollis H. Allen



November 1995 – Final Report

The following two letters used as part of the number designating technical reports of research published under the Wetlands Research Program identify the area under which the report was prepared:

	Task		Task
CP	Critical Processes	RE	Restoration & Establishment
DE	Delineation & Evaluation	SM	Stewardship & Management

Wetlands Research Program

Technical Report WRP-RE-10
November 1995

Mitigated Wetland Restoration: Environmental Effects at Green Bottom Wildlife Management Area, West Virginia

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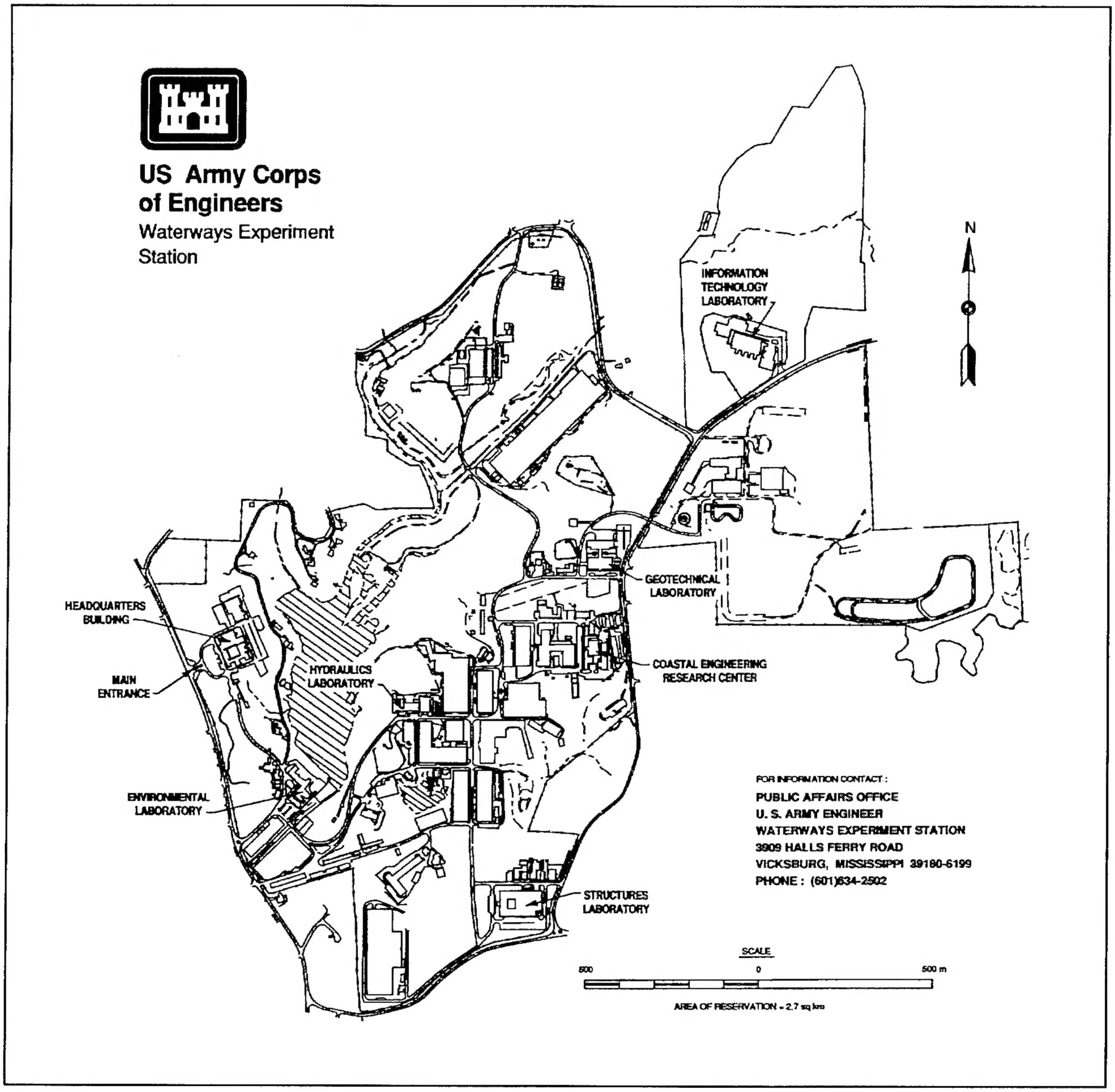
Final report

Prepared for U.S. Army Corps of Engineers
Washington, DC 20314-1000



Waterways Experiment Station Cataloging-in-Publication Data

Evans, Dan K.

Mitigated wetland restoration : environmental effects at Green Bottom Wildlife Management Area, West Virginia / by Dan K. Evans, Hollis H. Allen ; prepared for U.S. Army Corps of Engineers.

229 p. : ill. ; 28 cm. -- (Technical report ; WRP-RE-10) (Wetlands Research Program technical report ; WRP-RE-10)

Includes bibliographic references.

1. Wetlands -- West Virginia. 2. Wetland conservation -- West Virginia. 3. Restoration ecology -- West Virginia. 4. Wetland ecology. I. Allen, Hollis H. II. United States. Army. Corps of Engineers. III. U.S. Army Engineer Waterways Experiment Station. IV. Wetlands Research Program (U.S.) V. Title. VI. Title: Environmental effects at Green Bottom Wildlife Management Area, West Virginia. VII. Series: Wetlands Research Program technical report ; WRP-RE-10. VIII. Series: Technical report (U.S. Army Engineer Waterways Experiment Station) ; WRP-RE-10.

TA7 W34 no.WRP-RE-10

Corps of Engineers Research Report Summary, November 1995

Wetland Restoration

Mitigated Wetland Restoration: Environmental Effects at Green Bottom Wildlife Management Area, West Virginia (TR WRP-RE-10)

ISSUE:

Many of the nation's former wetlands have been lost for residential, commercial, or agricultural purposes. Restoration and information concerning the environmental impact of restoration efforts are critically needed to reclaim some of these valuable resources.

RESEARCH:

A comprehensive investigation involving nine different studies was initiated at the Green Bottom Wildlife Management Area (GBWMA) in West Virginia. Historical records, i.e., old newspapers, engineer maps, and aerial photographs, were analyzed to evaluate land use over time in the area. Vegetation and soil samples were collected using random sampling throughout the site. Resident populations of dragonflies, frogs, and grass pickerel were examined. Also the dynamics of twenty-five species of mosses and four species of liverworts were investigated.

SUMMARY:

Historical analysis revealed increased wetland destruction as farming intensified in the area. Vegetation analyses revealed the presence of seven vegetative types arranged along a moisture gradient. Soils were developing toward true wetland soils following 8 months of inundation. A species list as well as information concerning territoriality, mating behavior, and cannibalism in naiadal dragonflies was established. Eight species of frogs and toads were found to breed at GBWMA. A baseline for managing the reproductive activities of the grass pickerel at the GBWMA was established. The highest moss cover is from the families Amblystegiaceae and Brachytheciaceae. The liverwort with the greatest cover and largest number of species is from the family Ricciaceae. This comprehensive study offers information in a broader perspective than what is readily available in the literature.

AVAILABILITY OF REPORT:

This report is available on Interlibrary Loan Service from the U.S. Army Engineer Waterways Experiment Station (WES) Library, 3909 Halls Ferry Road, Vicksburg, MS 39180-6199, telephone (601) 634-2355.

To purchase a copy, call the National Technical Information Service (NTIS) at (703) 487-4650. For help in identifying a title for sale, call (703) 487-4780.

NTIS report numbers may also be requested from the WES librarians.

About the Authors:

Dr. Dan K. Evans is a Professor, botanist, and Project Director, Marshall University, Department of Biological Sciences, Huntington, WV. Mr. Hollis H. Allen is a forest ecologist, WES Environmental Laboratory. Point of Contact is Mr. Allen, Phone: (601) 634-3845.

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Preface

The work described in this report was authorized by Headquarters, U.S. Army Corps of Engineers (HQUSACE), as part of the Wetland Restoration, Protection, and Establishment of Wetlands Task Area of the Wetlands Research Program (WRP). The work was performed under Work Unit 32761 for which Dr. Mary C. Landin, U.S. Army Engineer Waterways Experiment Station (WES), was the technical manager. Ms. Denise White (CECW-ON) was the WRP Technical Monitor for this work.

Mr. Dave Mathis (CERD-C) was the WRP Coordinator at the Directorate of Research and Development, HQUSACE; Dr. William L. Klesch (CECW-PO) served as the WRP Technical Monitors' Representative; Dr. Russell F. Theriot (WES) was the Wetlands Program Manager. Dr. Landin was the Task Area Manager.

Participants in the study, in addition to the authors, included Messrs. Ben Borda, Wally Dean, and John Yeager, of the U.S. Army Engineer District, Huntington, West Virginia (CEORH). The Huntington District, in coordination with WES, contracted with Marshall University (MU) for the work described in this report under Contract Numbers DACW69-92-M-1662 and DACW69-93-R-0015. Mr. Robert Lazor of WES (CEWES-EP-W) was instrumental in facilitating the above initial coordination with the district.

This report is divided into chapters edited by Hollis H. Allen (EL). Each chapter was written by various individuals at WES and Marshall University, including the following: Chapter 1—"Overview of Wetlands Restoration Efforts and Effects at Green Bottom Wildlife Management Area," Mr. Hollis H. Allen (WES), Dr. Dan K. Evans, Mr. Tim J. Stark, Ms. Nicole Turrill, and Ms. Tonda Waugh (MU); Chapter 2—"Dynamics of the 20th Century Wetlands," written by Dr. Dan K. Evans, assisted by Ms. Nicole Turrill and Ms. Tonda Waugh (MU); Chapter 3—"Flora and Vegetation," written by Mr. Tim J. Stark under the direction of Dr. Dan K. Evans; Chapter 4—"Propagation of Selected Woody Plant Species in a Created Wetland," written by Mr. Jeffrey D. May (MU); Chapter 5—"Changes in Soil Physical and Chemical Characteristics," written by Dr. Frank S. Gilliam; Chapter 6—"Nitrogen Transformations," written by Dr. Frank S. Gilliam with assistance from Mr. Mark A. Fisher (MU); Chapter 7—"Bryophyte Communities," written by Kimberly Cunningham under the direction of Mr. Thomas E. Weaks;

Chapter-8—"Behavioral and Physiological Ecology of Dragonflies (Odonata: Anisoptera)," Dr. Donald C. Tarter and Ms. Lee Ann Mullins (MU); Chapter 9—"Preliminary Observations on the Reproductive Biology of the Grass Pickerel, *Esox Americanus Vermiculatus* Lesueur," written by Dr. Donald C. Tarter (MU) and Ronald C. Tipton; Chapter 10—"Natural History and Ecology of Anurans," written by Mr. Thomas K. Pauley assisted by Mr. James W. Barron (MU).

The report was written under the direct supervision of Mr. Hollis H. Allen, Acting Chief, Stewardship Branch, and under the general supervision of Dr. Robert M. Engler, Chief, Natural Resources Division, and Dr. Edwin A. Theriot, Assistant Director, EL, and Dr. John Keeley, Director, EL. The authors acknowledge assistance provided by Dr. Robert Maslowski, Huntington District; Ms. Anne Hockenberry, for her generous help with soil extraction; and Ms. LuAnne South for typing several reports and Mr. L. Douglas Whitaker, EL, for editorial support.

At the time of publication of this report, Director of WES was Dr. Robert W. Whalin. Commander was COL Bruce K. Howard, EN.

This report should be cited as follows:

> Evans, D. K., and Allen, H. H. (1995). "Mitigated wetland restoration: Environmental effects at Green Bottom Wildlife Management Area, West Virginia," Technical Report WRP-RE-10, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

Conversion Factors, Non-SI to SI Units of Measurement

Non-SI units of measurement used in this report can be converted to SI units as follows:

Multiply	By	To Obtain
acres	4,046.873	square meters
feet	0.3048	meters

1 Overview of Wetlands Restoration Efforts and Effects at Green Bottom Wildlife Management Area[1]

Introduction

This report includes several studies that document changes in plant and animal communities and soils as a function of natural and man-made changes of a remnant wetland located along the Ohio River. The historic wetland, called Green Bottom, was converted to agricultural fields in the early 1900's, with only remnant wetland areas remaining, largely riparian streams. Now called the Green Bottom Wildlife Management Area (GBWMA), it is located 26.7 km north of Huntington, WV (Figure 1). Most of the 338-ha area occurs between State Route 2 and the Ohio River in Cabell and Mason counties, just 13.4 km downstream of the Corps of Engineers Gallipolis Lock.

The site selection, acquisition, development, and management of the GBWMA is a result of joint efforts by the U.S. Army Engineer District, Huntington, West Virginia Department of Natural Resources (WVDNR), and the U.S. Fish and Wildlife Service (USFWS). The area was purchased and established by the Corps of Engineers to mitigate impacts to wildlife and habitat incurred by implementation of the Gallipolis Locks and Dam Replacement Project. It is now managed by the WVDNR as a state hunting and fishing area under a lease agreement with and overview responsibility of the Huntington District. The area has been an important research, teaching, and recreation resource for nearby Marshall University (MU), environmental groups, and interested citizens.

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[1] Hollis H. Allen, M.S.; Dan K. Evans, Ph.D.; Tim J. Stark, M.S.; Nicole Turrill, M.S.; Tonda Waugh.

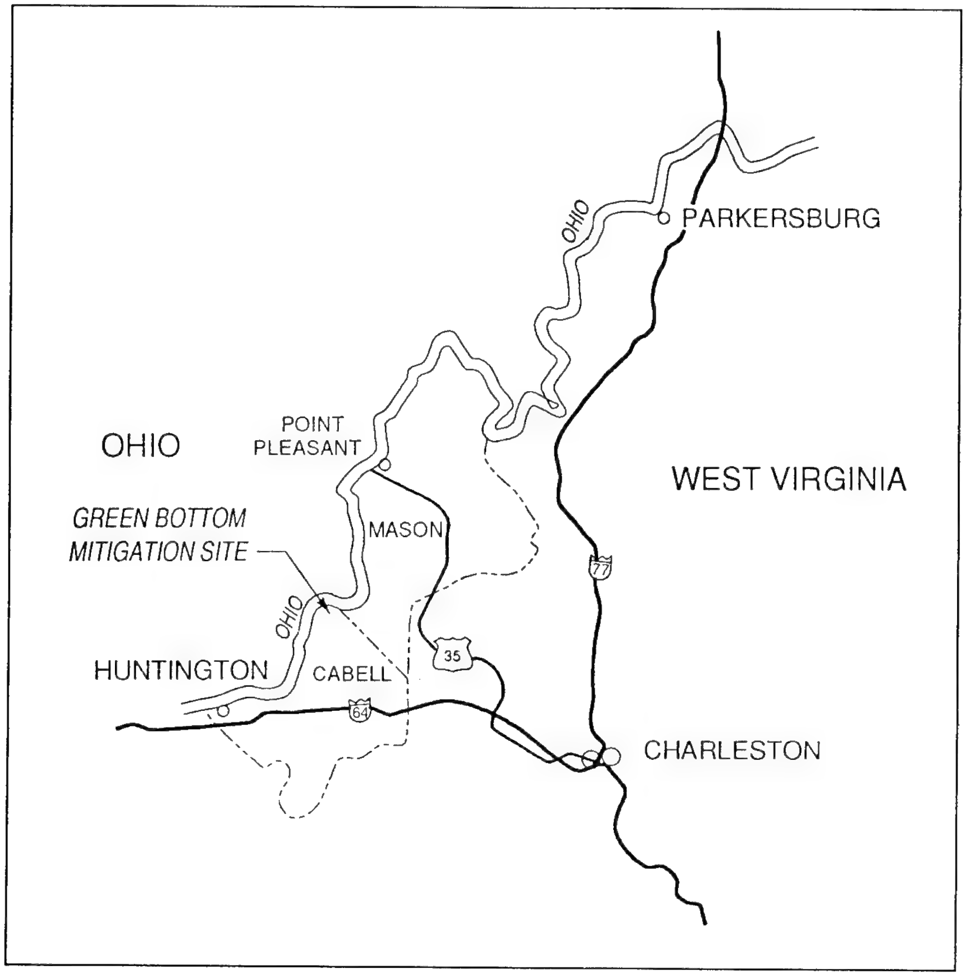

Figure 1. Map of GBWMA

Study Area

GBWMA is located 19.6 km north of Huntington, WV. GBWMA is contained in 338 ha, 58 of which are wetlands (WVDNR 1991). The wetlands are located mainly between State Route 2 and the Ohio River in Cabell and Mason counties. Terrestrial inputs (runoff) and drainage controls, such as beaver dams and human construction, are constantly influencing the hydrology and wetland acreage of the swamp. There are four wetland types in GBWMA: seasonally flooded flats, inland open fresh water, shrub swamp, and wooded swamp. Permanently inundated areas with a full-to-loose or punctuated woody canopy are classified as swamps (Stark 1993). The 10-ha shrub swamp and the 0.4-ha wooded swamp are located 14.3 km east of Lesage, WV, adjacent to U.S. 2 (Figure 2). The inland open fresh water is located 13.2 km east of Lesage, WV, adjacent to U.S. 2 (Figure 2). The distinct historical marker is the General Jenkins House. The seasonally flooded flats are located 14.8 km

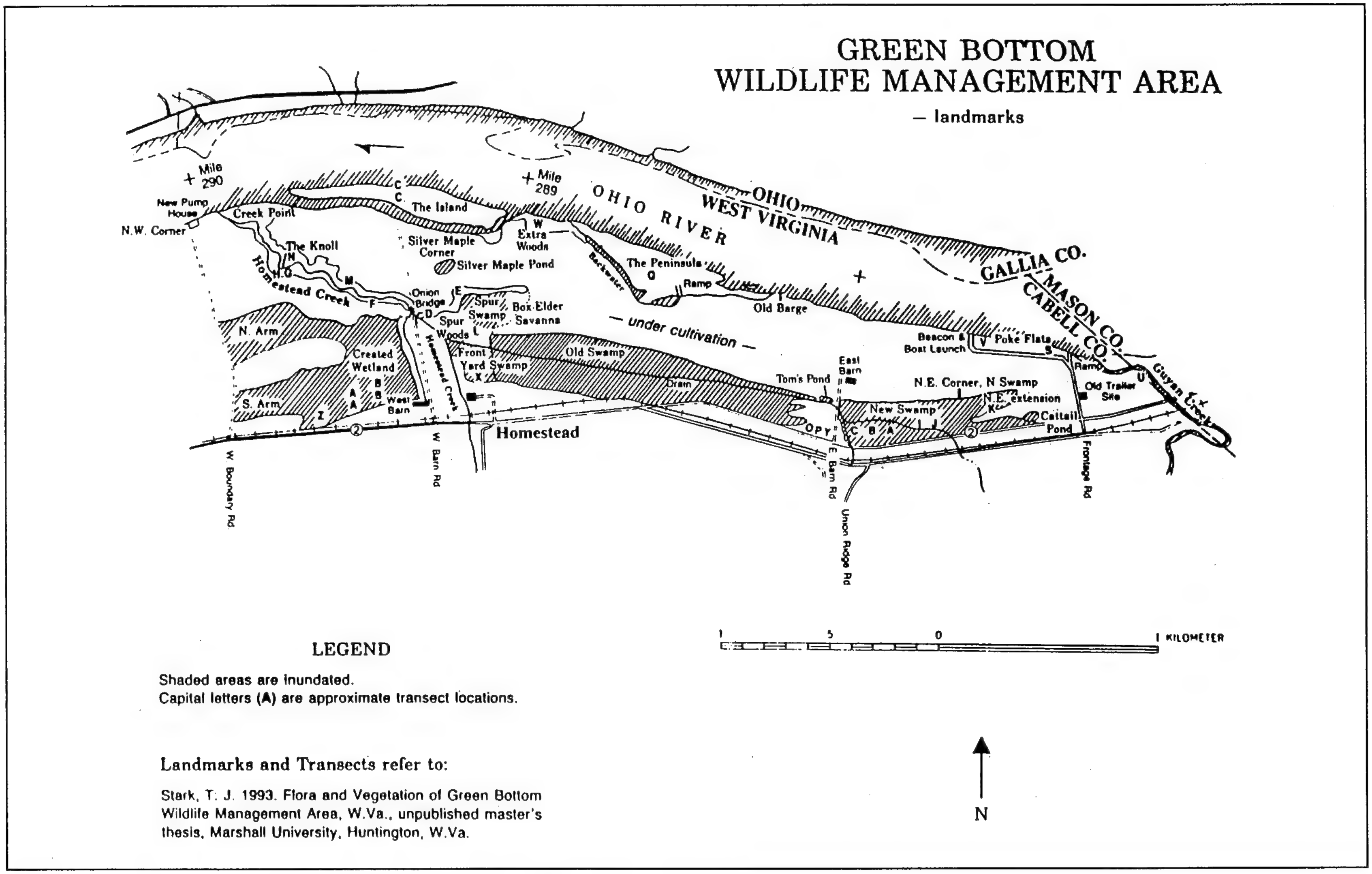

Figure 2. Map of GBWMA indicating site locations (■ represents the wooded swamp and where the monthly samples were taken)

east of Lesage, WV, adjacent to U.S. 2, at the first left entrance road (Figure 2). This site is located close to the farm pond.

Climate

Western West Virginia has a temperate, continental climate brought from the interior by prevailing southwesterly winds. Figure 3 summarizes 20-year daily precipitation and temperature readings taken at Huntington, WV, for the period ending December 1980. Winter months are cold and have a moderate amount of snowfall with an average of 66 cm per year. Summers are fairly warm on hillsides and very warm in the valleys (Cole 1989). Annual average temperatures are approximately 12.8 °C, with maximum temperatures reaching above 37.8 °C. The average temperature of the winter months is 2 °C while an average of 22.8 °C occurs in summer (Cole 1989). The total annual precipitation is approximately 104.5 cm with 55 percent typically falling in April through September. The average relative humidity in mid-afternoon is about 60 percent. Humidity is higher at night, and the humidity at dawn is near 80 percent (Cole 1989). Wind is from the southwest and reaches its highest average of 12.9 kph in spring (Cole 1989).

Physiography and geology

This part of the Ohio River Valley falls within the Western Allegheny Plateau ecoregion as defined by the U.S. Environmental Protection Agency (USEPA) (Omernik 1987). In making its determinations, USEPA considers land surface form, potential natural vegetation, soils, and land use. The rocks of most of this region are late Pennsylvanian or early Permian systems, with northern Cabell County identified as part of the Monongahela group. This group dates to the late carboniferous period, or first coal age, when expansive "coal swamps" existed along the eastern and southern edges of the North American inland sea. Nonetheless, rocks here are formed of terrestrial sediments, the youngest of the Appalachian geosyncline (Foster 1988).

Although not covered by the Pleistocene glaciers, the flowering plants of the Ohio Valley were greatly disturbed by the voluminous melt of the retreating Wisconsin ice. The formation of the Ohio Valley, with its broad expanse of deeply sedimented floodplains, is considered to be a result of this event (Foster 1988, La Rocque and Marple 1955). This area may therefore be exceptional to Braun's (1950) determination of the persistence of southern mixed mesophytic forest communities on the unglaciated Allepheny Plateau during the Pleistocene epoch.

Flooding

Local meteorology may be less defining of the vegetation near waterways fully controlled by highlift dams. Elevation at Green Bottom varies less than

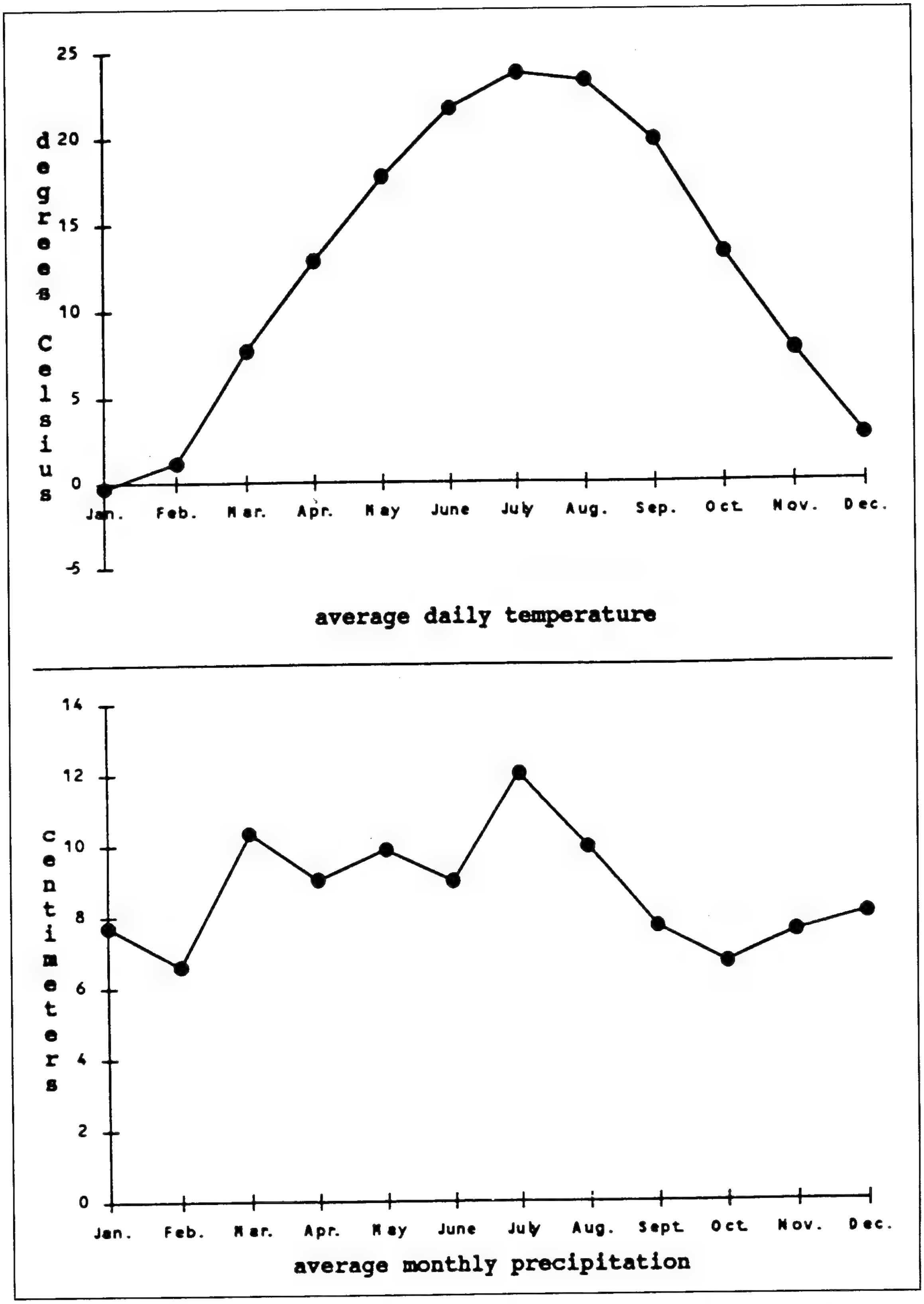

Figure 3. Summary of average daily temperature and average monthly precipitation readings for the period 1961-1980, taken at Huntington, WV (adapted from Cole 1989)

5 m to either side of the median 164 m. With little or no slope-aspect considerations, microelevation and the controlled flooding regime become important determiners of plant colonization success. Pool levels of the Ohio River system have been regulated for most of this century. Quantitative investigation of seasonal pool fluctuation is beyond the scope of this work, though it can be noted that a great portion of the floodplain exposed in 1900 is now permanently inundated (Ely 1992). Riverside mudflats and sandbars still experience seasonal inundation within these navigation pools. Most of the site, however, lies above allowed pool fluctuations. Terrestrial inputs (runoff) and drainage controls, such as beaver dams and human construction, influence the hydrology of these latter regions.

Soils

The deep, loamy soils associated with GBWMA drain poorly and not only allow for the 52.6 ha of swamp but also for numerous ponds and vernal pools. The U.S. Department of Agriculture (USDA) Soil Conservation Service of Cabell County describes the area as a combination of four soil orders: alfisols, mollisols, entisols, and inceptisols, dominated by the Ashton-Huntington-Melvin series (Cole 1989). These are floodplains of varying elevation and hydrology. All are dark, medium-textured, mesic to aquic alluvium. Only Melvin (Me) are classified as hydric soils (Figure 4).

Topography

GBWMA is a 338-ha area along the Ohio River, 25.7 km north of Huntington in Cabell County, WV (82 °14'00" West, 35 °00'30" North) (WVDNR 1991). The area can be roughly described as a riparian floodplain supporting swamps in several stages of succession (Stark 1993). At the foot of ancient river bluffs, it is separated from the river by natural terraces, wet old fields, marshes, and riverside mud flats. The most prominent habitat feature is Green Bottom Swamp, an approximately 60-ha native freshwater wetland drained by a creek surrounded by a narrow remnant stand of bottomland hardwoods. A deep-water side channel, abandoned oxbow, ponds, and a near-shore island add to the wetland diversity. The swamp is drained by a creek surrounded by a narrow bottomland hardwood forest (Stark 1993).

Vegetation

The current beaver activity and Corps of Engineers levee construction are rapidly increasing the actual wetland area causing the atypical occurrence of such woody trees as *Acer negundo*, *A. saccharinum*, and *A. saccharum* in standing water. These trees will soon be examples of the irregular woodiness that can be taken as an indicator of succession toward the swamp community.

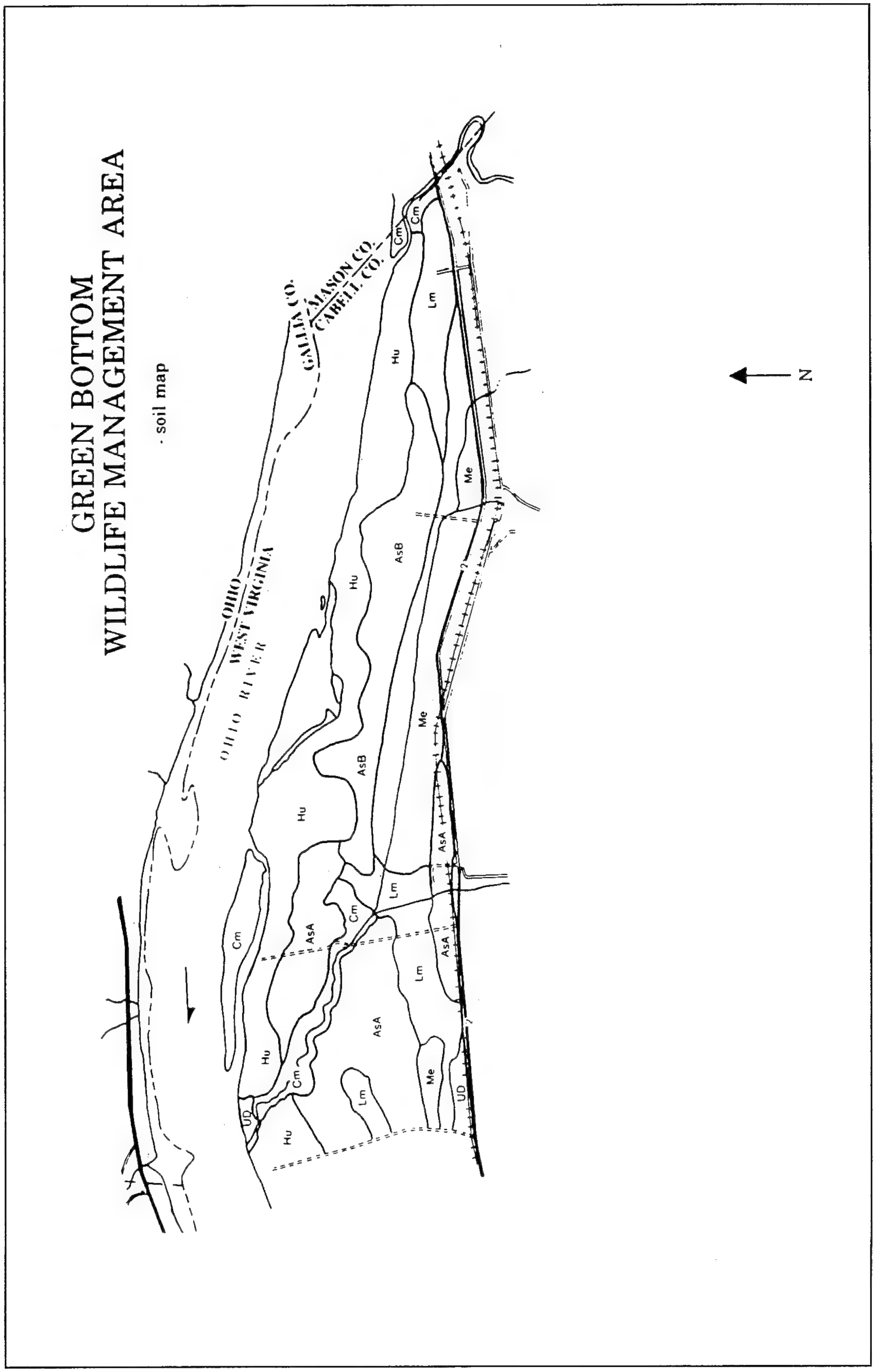

Figure 4. USDA soil map units at GBWMA (adapted from Cole 1989)

Buttonbush (*Cephalanthus occidentalis*), a wetland shrub, defines and dominates the deepest and wettest areas, while *Lemna minor*, *Spirodela polyrhiza*, and *Wolffia* sp. cover the majority of the surface water. *Carex* species thrive in and around the swamp on the soft, marshy soil, while marsh mallow (*Hibiscus moscheutos*) enclose the swamp with a magnificent arrangement of white blossoms.

Wildlife

GBWMA is comprised of a diverse array of wildlife. The swamp provides an excellent habitat for amphibians such as spotted salamander (*Ambystoma maculatum*), Jefferson salamander (*Ambystoma jeffersonianum*), red-spotted newt (*Notophthalmus v. viridescens*), wood frog (*Rana sylvatica*), pickerel frog (*Rana palustris*), leopard frog, (*Rana pipiens*), bullfrog (*Rana catesbeiana*), and spring peeper (*Pseudacris crucifer*). Reptiles such as the midland painted turtle (*Chrysemys picta marginata*) and the snapping turtle (*Chelydra serpentina*) can also be found in abundance. Many aquatic insects including dragonflies, damselflies, mayflies, water boatman, and hymenopterons find refuge among the rushes and sedges. Certain fishes including bowfin (*Amia calva*), bluegill (*Lepomis machrochirus*), largemouth bass (*Microptreus salmoides*), green sunfish (*Lepomis cyanellus*), black and white crappie (*Pomoxis nigromaculatus* and *P. annularis*), carp (*Cyprinus carpio*), grass pickerel (*Esox americanus vermiculatus*), central mudminnow (*Umbra limi*), and black and yellow bullhead (*Ictalurus melas* and *I. natalis*) are known from the area (McGinn-Daniels 1992). This area provides a unique habitat for several bird species including the great blue heron (*Ardea herodias*), green heron (*Butorids striatus*), wood ducks (*Aix sponsa*), Canadian geese (*Branta canadensis*), or red-winged blackbirds (*Agelaius phoeniceus*). Larger animals such as the muskrat (*Ondatra zibethicus*), beaver (*Castor canadensis*), and white-tailed deer (*Odocoileus virginianus*) can also be found within the confines of GBWMA.

Land history

Green Bottom has a rich history. This area has 18 recorded archaeological sites. Six of these sites will be nominated to the National Register of Historic Places. One, the Clover site, which dates back to 1600 A.D., is a candidate for listing as a National Landmark (WVDNR 1991).

GBWMA was used 12,500 years ago by the Paleo-indians who passed through in search of caribou. Intensive use of GBWMA took place in the late Archaic Period, around 5,000 years ago. Historic references indicate that North American Indians used burning as a land management technique. During this period, experimentation took place which led to the development of the Eastern Agricultural Complex. This complex included such things as gourds, sunflower, lambsquarter, little barley, smartweed, and maygrass. By 1200 A.D., the woodland horticulture was replaced by large Fort Ancient

Villages. The principal crops included corn, beans, and squash (WVDNR 1991).

Thomas Hannan in 1796 was the first European settler at Green Bottom. In 1825, William A. Jenkins purchased 1,779.9 ha which included the GBWMA site. When William Jenkins died, the estate was divided among his three sons. Albert Gallatin Jenkins inherited the house and the eastern third of the estate (WVDNR 1991). The Jenkins House is listed on the National Register of Historic Places and is presently used as the residence for the DNR Area Manager (WVDNR 1991).

Even though the Jenkins Estate was in litigation during the late 1800's, the area continued to develop into prime farmland. There is indication that the major swamps in the project area were drained between 1883 and 1895 (WVDNR 1991).

The earliest photographic record of GBWMA is an aerial photograph taken in 1934. This photo indicates that the area occupied by Green Bottom Swamp was drained and used as a pasture and an orchard. Since 1950, three events occurred which raised the water level and caused the swamp to redevelop: the construction of a farm road, the construction of State Route 2, and colonization by beaver. Approximately 3.24 ha of the swamp were lost to the construction of State Route 2 in 1975. Over 85 percent of the bottomland forest in the swamp was dead or dying by 1989, a result of inundation caused by beaver (WVDNR 1991).

A mitigation plan was developed by the Department of Natural Resources (DNR), FWS, and the Corps of Engineers. This plan was provided to Congress in the December 1980 Fish and Wildlife Coordination Act Report. The plan recommended the acquisition and management of the Green Bottom Swamp area for wildlife and for hunting and fishing, as well as for uses such as bird watching, photography, and nature study (WVDNR 1991).

DNR signed a 25-year lease with the Corps of Engineers for the management of the GBWMA mitigation lands on 20 February 1989. The lease stipulates that the area will conform to the regulations prescribed by the Secretary of the Army and the Chief of Engineers to govern the public use of the area.

Literature Review

This research is the latest of more than 20 works addressing various botanical, zoological, ecological, and anthropological aspects of the area produced in the last 15 years (cf Evans 1991). Little is available regarding vegetation of the GBWMA until 1934, the date of the first aerial survey of the middle Ohio River. Recent vegetation studies in the GBWMA include classification of the swamp community by Liu (1991), a floristic study and plant community classification by Stark (1993), and a study of remnant bottomland forests by Furry

(1978); Evans and Taylor (1978) reported several species of vascular plants rare to West Virginia at the site. Cunningham and Weaks (1994) classified bryophyte communities in the older swamp. Gilliam (1993) demonstrated hydric soil development in newly impounded areas that comprise a part of onsite mitigated wetlands. Hill and Taylor (1982) showed the negative effect of highway construction on hydrology in Green Bottom Swamp.

Wetland Management and Restoration Efforts

The Corps of Engineers recently implemented a management plan that called for considerable habitat modification. The plan called for:

- Planting upland trees and shrubs to create wildlife habitat diversity.
- Developing at least some additional 28.8 ha of wetlands from cultivated lands through the use of dikes, weirs, and plantings.
- Managing water levels in order to increase wetland and waterfowl related habitat.

As a part of the plan, no construction activities were permitted in the existing wetland area. A preservation weir was constructed immediately downstream of the existing wetlands, which were created by a beaver dam, to maintain the existing water surface elevation of 544.0 ft[1] mean sea level (msl)[1] datum. The weir was designed and constructed to blend with the natural environment and yet be durable.

Additional wetlands were developed by the construction of earthen levees located in the existing wetland pool. The levees have a top width of 12 ft which allows access for maintenance vehicles. Each levee has a minimum of 2 ft of freeboard to prevent overtopping during high water periods. The newly developed wetlands cover an area which was cultivated for numerous years and has been environmentally and historically disturbed.

Water needs are supplied by pumping river water into the area, thus providing a reliable water source and promoting continual wetland management capability. The maximum depth of water in the developed wetland area is 1.5 m with an average depth of 0.6 to 0.9 m.

The use of concrete flash-gate water control structures which incorporate a stop-log and spillway system facilitate water-level management and maintenance by the WVDNR. Small incremental changes in the water levels are possible through the use of several different heights of stop-logs. When a

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[1] A table of factors for converting non-SI units of measurement to SI units is presented on page xvii.

change in water level is desired, the stop-logs can be removed and installed quickly. Each stop-log is equipped with an eye-bolt screw at each end so that hooks can be used for easy removal. The stop-logs are numbered and sized accordingly to allow rapid changes.

Environmental Effects Resulting from Restoration

This report presents the results of nine independent research efforts that evaluated the environmental effects resulting from the restoration of GBWMA.

a. "Dynamics of the 20th Century Wetlands" describes land use at GBWMA in the late 19th and 20th centuries. Wetlands are evaluated with literature accounts and ground photographs, along with habitat and land-use maps drawn from aerial photographs. A 59-year period, 1934 to 1994, is examined for diversity and size of wetland communities.

b. "Flora and Vegetation" offers a comprehensive description of the vascular plants and plant communities at GBWMA. Seven vegetation types are defined and arranged along a moisture gradient: streamside forest, river flats, beach, new swale, old swale, marsh, and swamp.

c. "Changes in Soil Physical and Chemical Characteristics," examines changes in several physical and chemical parameters, including soil oxidation-reduction potential and texture, organic matter, pH, extractable macronutrients, and extractable micronutrients.

d. "Propagation of Selected Woody Plant Species" assesses the practicality of establishing five woody species by direct planting of cuttings gathered from a nearby bottomland forest. The five species consist of two tree species and three shrub species.

e. "Nitrogen Transformations" evaluates nitrogen (N) availability using *in situ* incubations of soils taken from three distinct habitat conditions based on degree of inundation during wetland creation.

f. "Bryophyte Communities" presents the dynamics of 25 species of mosses and four species of liverworts observed in eight wetland plant communities located within the floodplain of the Ohio River.

g. "Behavioral and Physical Ecology of Dragonflies (Odonata:Anisoptera)" provides a species list of resident odonate populations within GBWMA prior to habitat modification and discusses the magnitude of territoriality in adult dragonflies.

h. "Preliminary Observations on the Reproductive Biology of the Grass Pickerel, *Esox americanus vermiculatus* LeSueur" elucidates the spawning activities of the grass pickerel. It establishes baseline data for

managing reproductive activities of the local population and enhances the data base on the undetermined status of the grass pickerel.

i. "Natural History and Ecology of Anurans" presents emergence from hibernation and calling period (breeding period) for eight species of toads and frogs. More specifically, it addresses ecological factors and interactions between *Rana pipiens* (northern leopard frog) and *R. palustris* (pickerel frog).

2 Dynamics of 20th Century Wetlands[1]

Introduction

Background

Little information is available regarding vegetation of GBWMA until 1934, the date of the first aerial survey of the middle Ohio River. Recent vegetation studies in GBWMA include classification of the swamp community by Liu (1991), a floristic study and plant community classification by Stark (1993) and a study of remnant bottomland forests by Furry (1978). Evans (1978) and Evans and Taylor (1978) reported rare vascular plants from the site. Cunningham and Weaks (1994) classified bryophyte communities in the older swamp. Gilliam (1993) demonstrated hydric soil development in newly impounded areas that comprise a part of onsite mitigated wetlands. Hill and Taylor (1982) showed the negative effect of highway construction on hydrology in Green Bottom Swamp.

Research objectives

The purpose of this research is to describe land use at GBWMA in the late-19th and 20th centuries. There are two specific objectives of the study:

a. To document wetland habitat in GBWMA through the use of aerial and ground photography, literature accounts, and oral history in the 20th century.

b. To demonstrate the dynamics of wetland habitats in GBWMA over time.

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[1] Dan K. Evans, Ph.D.; Nicole Turrill, M.S.; Tonda Waugh.

Methods and Materials

Newspaper articles from the period 1853 to 1895 and oral history describe land use and farming practices impacting wetlands in the late 19th and early 20th centuries.

Recent literature, oral history, and engineering maps, along with ground and aerial photographs from the period 1904 to 1993 were used in describing the wetlands of the 20th century.

Vegetation and land use maps were drawn on mylar from selected aerial photographs. From these, the size of wetland environs was assessed and habitat dynamics determined.

Results and Discussion

Pre-20th century wetlands

The best accounts of pre-20th century vegetation associated with the current GBWMA come from local newspaper articles and oral history. The newspaper *Guyandotte Herald*, Guyandotte, Cabell County, Virginia (1853), describes some 600 acres of land for sale at the mouth of the Little Guyandotte River (now Guyan Creek) at the upper end of the famed Green Bottom, Virginia. The description declares that the Ohio River bottomland is in a high state of cultivation and that it supports a steam mill for manufacturing lumber. Additionally, the land is described as having six frame houses with good barns and stables.

Later newspaper accounts appear in *The Huntington Advertiser*, Huntington, WV (1895). Here the Upper Greenbottom is depicted as a mecca for corn and other farm products. Further description relates to 300 acres just below the Little Guyan River. The article states that managers of the farm have brought about improvements by draining swamps and redeeming every acre of the land. The article goes on to say that, despite a dry season, the farm has produced 1,200 bushels of wheat, 80 tons of clover hay, 30 tons of bailed straw and 8,000 bushels of excellent yellow corn. Further, the farm provides grazing for 30 head of cattle, 8 horses, 30 hogs, and 40 sheep. Accounts of farms adjacent to those in the Green Bottom area reveal intensive farming activity including fruit production. Evidence suggests that little natural area remains.

20th century wetlands

The first ground photograph providing information on land use and vegetation in GBWMA was taken in 1904 (Figure 5). It is interesting to note the condition of what later came to be known as Green Bottom Swamp. The "swamp," located to the right-front of the Jenkins home (Figure 5), is

Figure 5. 1904 photograph of Green Bottom area (Courtesy of Robert Maslowski)

apparently without any standing woody vegetation. Although snow covers the ground, conditions indicate that the area has been cleared and probably drained. Corn shocks in adjacent fields suggest that the "swamp" remained too wet for row crops. The area directly in front of the home (Figure 5), currently classified as marsh with standing water, is pictured as a cultivated field with corn shocks scattered throughout. These conditions, observable in the photograph, agree with newspaper accounts of 1853 and 1895 that report efforts to convert wetland areas to farm production.

The first aerial survey of the middle Ohio River and the adjacent floodplain was made in 1934. The resulting photograph of Green Bottom shows remnant vegetation and land use (Figure 6). Perhaps most striking are the efforts to drain the swamp. A drainage ditch runs the length of the swamp with lateral ditches throughout. Dry ridges were created when the lateral ditches were dug, and fruit trees have been planted on several of them. An examination of stereo-pairs of the photograph indicates that the swamp supports woody, probable scrub-shrub vegetation. Current conditions suggest that button-bush (*Cephalanthus occidentalis*) probably occupied the wettest parts. No large trees are present. No field tile have been found to date. Evidence suggests that between 1904 and 1934, the swamp was allowed to regenerate toward a wetter environment.

Figure 6. 1934 photograph of Green Bottom area (Ohio River Aerial Survey, Huntington, WV, 1934)

Appendix A offers vegetation maps drawn from aerial photographs of the Green Bottom area during the period from 1934 to 1993. Table 1 summarizes the diversity and dynamics of wetland habitats during the 60-year period.

The vegetation map drawn from the 1934 photograph shows the extent of wetland habitats throughout the Green Bottom area (Figure A1). A total of 194.9 acres of wetlands is mapped. Intensive efforts to place wetlands into farm production have reduced diversity in habitat. The Streamside Forest and Swale communities comprise the largest wetland habitats remaining in 1934.

Figure A2, drawn from a 1957 aerial photograph, shows a significant increase in wetland habitats since 1934, including streamside forest, swamp, and bottomland hardwood communities. River flats and beach communities, along with two side channels were created when sand was mined along the river shore in 1956. The large swale community, present in Figure 6, has been converted to cultivated land. Some 255.8 acres of wetlands are mapped.

The vegetation map seen in Figure A3 is drawn from a 1973 aerial photograph. A total of 339.4 acres of wetland habitat is mapped. The increase in wetlands over that of 1957 results largely from the increase in the swale, swamp, beach, and river flats habitats. Small ponds were created when one of

Table 1
Size and Diversity of Wetland Habitats in GBWMA

Habitat	Map Code	Habitat Size by Year, acres					
		1934	1957	1973	1984	1990	1993
Streamside forest	B	82.5	90.8	68.1	59.8	87.2	75.3
Swale	E	84.9	16.7	57.4	31.1	38.2	
Swamp	F	21.5	57.4	87.2	66.9	125.5	150.1
Bottomland hardwood	L	6.0	52.6	62.2	35.9		
Beach	A		8.4	14.3	3.6	4.8	16.7
River flat	C		29.9	45.4	32.3	55.0	43.0
Pond	D			4.8	7.2	7.2	7.2
Marsh	G				7.2	7.2	55.0
Mitigated wetland	J						84.9
Total Acres of Wetland		194.9	255.8	339.4	244.6	325.1	434.6

Note: Habitat size calculated from vegetation maps drawn from aerial photographs representing the period 1934 to 1993.

the river side channels filled in. Mr. James Knight[1] former owner of much of the Green Bottom area, relates that during the late 1950's and 1960's, there was less emphasis on farming the area. During this time, efforts to keep the swamp and adjacent wetlands dry were largely abandoned. Subsequently, drainage ditches filled with sediment, allowing the restoration of additional wetlands.

Figure A4, drawn from a photograph made during the middle Ohio River survey in 1984, reveals a loss in swale and swamp habitats. The 244.6 acres of mapped wetland represents a loss of 94.8 acres during 11 intervening years. Swale habitat was lost to renewed interest in farming. Highway construction in 1975 encroached on the Swamp and adjacent bottomland hardwood communities and negatively affected the hydrology in wetland habitats (Hill and Taylor 1982).

In 1990, GBWMA was under the management of WVDNR. Efforts were already underway to increase habitat for waterfowl and terrestrial game species (WVDNR 1991). Figure A5, from a 1990 aerial photograph, shows a significant gain in wetland habitat. The streamside forest habitat has been allowed to

[1] Personal Communication, 1980, James Knight, owner, Glenwood, WV.

encroach on adjacent cultivated fields. Most conspicuous is the increase in swamp habitat, attributable to an increase in water level resulting from new beaver dams. By early 1990, the bottomland hardwood habitat joining the swamp in Figure A4 had standing water throughout, and selected species of trees were experiencing die back. No effort has been made to destroy the beaver dams.

Figure A6 was drawn from maps used in mitigation planning for GBWMA. No aerial photograph is available that shows current wetland habitats. Water levels predicted for the mitigated wetlands were realized in 1993. The mitigated wetland of 84.9 acres represents the largest increase in wetland habitat for the Green Bottom area. With increased water level from beaver activity, swamp and marsh habitats continue to expand, replacing bottomland hardwood and swale communities. The loss of river flats and the gain of beach habitat is likely an artifact that results from mapping from engineering maps rather than from aerial photographs. A total of 434.6 acres of wetland habitat are mapped.

Summary

Late 19th century newspaper accounts and early 20th century ground photographs of GBWMA reveal significant wetland destruction as farming intensity increased.

Table 1 summarizes the size and diversity of wetland habitats over time in the Green Bottom area. Wetland habitat increased from 194.9 acres in 1934 to 434.6 acres in 1993, a growth of 123 percent in a 59-year period.

Wetland habitat diversity increased steadily from three communities in 1934 to seven in 1993. Swale communities gave way to marsh habitat and bottomland hardwood to swamp with a marked increase in water level from 1990 to 1993. The single most significant increase in wetland habitat was due to mitigation. A combination of wetland restoration, creation, and enhancement resulted in 84.9 acres of quality wetlands.

3 Flora and Vegetation[1]

Introduction

Purpose of study

This research is a description of the vascular plants and plant communities at GBWMA. It is intended to provide the comprehensive baseline information necessary for future research and successful management at this and comparable sites. It is the latest of, and corollary to, the more than 20 works about various botanical, zoological, ecological, and anthropological aspects of the area produced in the last 15 years (cf. Evans 1991). Liu (1991) described the vegetation of the oldest section of deep- and open-water swamp at Green Bottom.

Objectives

There are four main objectives of the research on flora and vegetation:

a. To quantitatively sample all apparent vascular plant communities; to characterize the vegetation.

b. To describe the ecology of the defined plant communities in terms of hydrological and soil texture gradients.

c. To compile an annotated catalogue and voucher specimens of the vascular flora.

d. To characterize the flora in terms of rarity, wetland status, obligation to habitat, and geographical affinity.

It is expected that these descriptions will reveal distinct, consistent plant community characteristics and provide quantitative correlations between the plants and observed environmental variables.

---

[1] Tim J. Stark, M.S.; Dan K. Evans, Ph.D.

Methods and Materials

Field collections were made from February 1992 through March 1993. Visits to the site from May to September averaged three per week. Redundancy due to the compactness of the study area allowed for sufficient characterization of the flora and plant communities after only one year.

Vegetation

Sampling methods. Viewing the distribution of species as a continuum (Gleason 1953), the characterization of communities is a prejudicial, arbitrary activity. Thus, clear understanding of sampling and analysis methods becomes extremely important (Barbour, Burk, and Pitts 1987). While the avoidance of bias is increasingly valued in the literature, true objectivity is unattainable in theory and practice. Direction and flexibility in sampling style and data analysis is required to test hypotheses concerning the influence of environmental gradients, the extreme physiographic variability of natural sites, and the expected mosaic pattern of plant associations within a given site type (Daubenmire 1968).

A stratified random location of sample points was made within gross community types chosen for visibility, unique physiography, and floristics. Care was taken to err on the side of repetition; it was expected that quantitative analysis of the collected data, by finding considerable similarity between sampled areas, would reduce rather than increase the number of vegetative communities finally reported. All type areas were sampled to the point of diminishing return of new information. Developing species lists and direct analyses of environmental gradients were consulted to reduce sampling redundancy.

The number and diameter at breast height (dbh) of all trees (woody species 10 cm dbh) were recorded from 10 m square plots located at regular intervals along one or more transects stratifying the gross community type. Shrubs (woody species 10 cm dbh and 1 m in height) were counted in these same plots and assigned one of six classes based on their height to the nearest meter, the smallest class being all shrubs 1 m to < 2 m in height, and the largest being individuals taller than 6 m. A single 1 m^2 subplot was randomly placed within each quadrant of the larger plots and the included herbaceous species (all plants <1 m in height) were sampled using a modified Daubenmire cover class scale (Mueller-Dombois and Ellenberg 1974). Because of their small size and great density, nonrooted (floating) plants were described from 0.06 m^2 plots nested within the herb plots. There is well-founded support of the standardized 0.1 ha Whittaker (1978) method (Gauch 1989); however, plots of this magnitude could not be fitted into the often narrow sampling areas. To accommodate the shape of the natural sample sites, the dimensions (but not the area) of some woody species plots were modified.

Data analysis. Multivariate analysis of data elicits community structure about which hypotheses may be tested (Gauch 1989). It bridges the gap between the Humboltian idea that no thing or action should be considered in isolation (Jongman, Ter Braak, and Van Tongeren 1987), and the human necessity to describe everything as a succession of individual thoughts. This synthesis is achieved through the combined use of classification, ordination, and correlation techniques. A standard procedure includes initial clustering of stands into a manageable number of groups, scoring of those groups through some form of multiple least-squares regression, and comparison of those axes to environmental scores for the same stands.

Herbaceous layer data from all subplots were classified by the divisive, polythetic, hierarchical computer algorithm TWINSPAN (Hill 1979b). TWINSPAN employs separate reciprocal averaging (RA) ordinations at each level of division. Final distribution of samples thus indicates absolute rank but not relative distance along a single gradient. Detrended correspondence analysis (DCA) (Hill 1979a, Hill and Gauch 1980), an improved ordination technique (Ter Braak and Prentice 1988), was used to spread the resultant communities within a single unified coordinate system, thus complementing the TWINSPAN analysis. Pearson product-moment correlation of ordination scores to environmental data then provided a direct gradient analysis of the communities. For a comprehensive review of multivariate techniques, see Ter Braak and Prentice (1988).

Species at all levels were described to frequency, and as either basal area (trees), density (shrubs), or average cover class (herbs). Respective relative values and a summary importance value were then calculated, with modifications, following McIntosh (1957). This provided a basis for classical analysis of community structure. Complete plot values for all herbaceous taxa are on file at the U.S. Army Engineer Waterways Experiment Station (WES), Vicksburg, MS, and are available upon request.

Soils. A 10 cm core sample of the eluvial (A) soil horizon was taken from each 1-m^2 quadrat. Texture analysis followed the method of Bouyoucos (1951).

Flora

The analysis of plot data contributed significantly to the cataloging task. The annotated catalogue, on file at WES, is a vouchered flora of GBWMA amended with precise element locations and ecology. It is constructed as a characterization of the vascular plant species complementary to the quantitative ecology described in the vegetation chapter of this work.

Voucher specimens of the author's collections are housed in the Marshall University Herbarium (MUHW). Voucher locations of additions to the final list from other sources are noted in the catalogue. All state records were noted and conveyed to the Office of the State Natural Heritage Program, along with

desired duplicate specimens. State ranking of rare and endangered species follows the latest revision of the state checklist from that office.

Wetlands. Wetland definition is improving through standardization (Mitsch and Gosselink 1986). The FWS now maintains the National List of Plant Species That Occur in Wetlands (Reed 1988). Plants on this list are defined as "...species that have demonstrated an ability (presumably because of morphological and/or physiological and/or reproductive strategies) to achieve maturity and reproduce in an environment where all or portions of the soil within the root zone become, periodically or continuously, saturated or inundated during the growing season" (Huffman 1981, in Reed 1988). All species were categorized as to the degree of their affinity to a wetland environment. This list was consulted, in combination with the Corps of Engineers Wetland Identification Manual (Environmental Laboratory 1987), to determine the Federal wetland status of the GBWMA flora.

Data analysis. Calculation of community similarity used the methods of Sorenson (Mueller-Dumbois and Ellenberg 1974) and Sokal and Sneath (1963). Floras are most valuable for comparison if they are comprised largely of native species. Determination of the geographical origin of all species in the catalogue was provided by the West Virginia State Natural Heritage Program.

Results and Discussion

Vegetation

Seven vegetation types, or communities, were defined from 147 sample points using TWINSPAN: beach, streamside forest, river flats, new swale, old swale, swamp, and marsh. These plant communities are arranged from left to right in Figure 7. All divisions continued to the third level except in the definition of the beach community, which split off as a small group of six plots at level 2. Each plot assignment was evaluated through field observation. Thirteen of the plots initially assigned to the river flats group formed a subgroup of disturbed area, or waste place, plots that did not fit the otherwise recognizable community. These anomalous plots were removed from further consideration in description of the vegetation.

Table 2 presents all herbaceous samples classified to type and includes species composition of each type by cover class. Dominant herb layer species, including indicator species as defined by TWINSPAN, are summarized in Table 3. Plots of the large streamside forest community are ordered in such a manner (Table 2) that they may be considered as three subgroups: lowland, or creekside, areas receiving frequent flooding (plots D1-H3); highland creekbank plots flooded only under severe conditions (plots L1-N3), and river berm (wooded upper slopes) forests separating the first agricultural terrace from the river beach (plots U1-W8). These finer distinctions were considered for mapping purposes only.

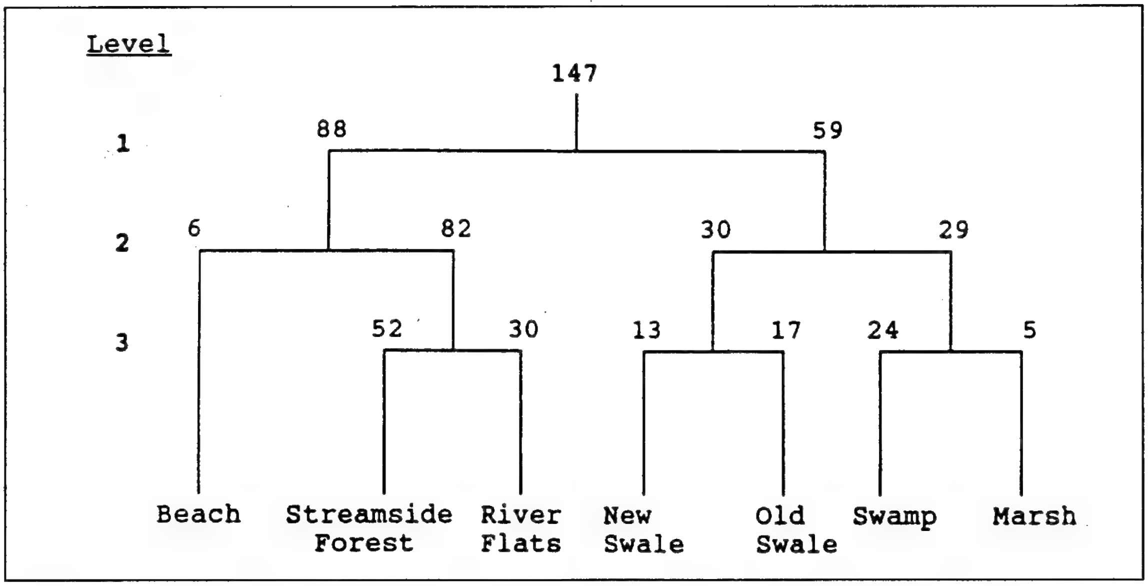

Figure 7. TWINSPAN classification of Green Bottom sample points (Number of plots assigned to each division is indicated. Thirteen anomalous plots were subsequently struck from the River Flats group)

Results

DCA analysis of the sample points are summarized in Figure 8. All seven vegetation types are well defined in the ordination space. First and second axis eigenvalues (0.911 and 0.695, respectively) indicate that these ordination scores account for most of the variation in the data. The first axis length was 3.9 standard deviations, indicating an almost complete change of species, or significant beta-diversity (Christensen and Peet 1984), along its gradient (Hill 1979b). The second axis length of 6.3 standard deviations indicates a greater beta-diversity along the gradient it defines.

Correlation of the DCA axes with environmental variables is summarized in Table 4. Sample scores along axis 1 are highly correlated with plot water depth ($r = 0.759$). Variation in community type is from the streamside forest samples with zero water depth (mean DCA axis 1 = 237.6) to swamp community samples with permanent inundation to 50 cm (mean DCA axis 1 = 830.0). Community means are reported and ranked in Figure 8.

A strong correlation also exists between the second axis and a measured sand-to-clay soil texture gradient (Table 3: $r = 0.527$ for sand, $r = -0.507$ for clay). However, Figure 8 shows that the vegetation types are not well-defined along this axis.

Table 2
Two-Way Indicator Species Analysis (TWINSPAN) Table

Community	A Beach	B Streamside Forest	C River Flats	D New Swale	E Old Swale	F Swamp	G Marsh
ACER SAC	2...2.	.....2.....	.22		.2		
AGRO CAP	22.252	.....2....					
AMOR FRU	22..22						
BIDE DIS	22.222				...22		
EUPA FIS	2....2		..2			...2	
EUPA SER	2.2.22				2		
PANI VIR	4.....						
RUME VER	2...22	.....2.....				2	
SALI EXI	222424						
ULMU SPP	.2....	...2				...2	
ACER NEG		..2.2.2.....2.2.22222	.2		.....2.2		
AGRO SPP		.....5225..2.2					
AMPH BRA	22	22422445522222222222....222..22.2222....244222..22..	2...22..2.......2		2		
APIO AME	2...4.	.....4....	2....2.......2				
ARUN GIG		.....24..52.......5					
ASTE LAT		2.22..2					
ASTE SPP		22...2.....2.2.....2.2	...2				
BIDE SPP		.222			2		
CALY SEP		.....2.....2....			2		
CAMP RAD	2....2	.....2.....2.22..22222	.242		2	.2.....2..	
CARE AMP		.....2.....222....22...2...2.222					
CARE GRA		.....2.2....222.....22...2	.2				
CINN ARU		.....2.....2.2.....2	..2		2	.....2..	
CRYP CAN		.222.22.24242.22224.....2...2..22.....2	.....2.2				
DESM CAN	2.....						
ELYM VIR		2222.554442222....545452 254555.42242.425555555555.45					
FEST OBT		245445442					
GALI APA		.....2.....222.222....2222222222	..2				
GEUM CAN		..22.....2..2.....22.2...2.....2.2					
GLEC HED		4422...44..2.....45..2...5...4..225454...4224	.2...2..2				
IMPA PAL		224445.452255555256....242.222424222.....225	2....2.....22.				
IPOM PAN		24222	..4		2		
LAPO CAN		....2.22242222..254.....22.....22.22..2524	....5...55..2242.				
LEER VIR	2...2.	...24.2222..45242.2.....22.....425	.5..545555555555544	.2...2	2	.....22..	
LONI JAP		...2.....4442					
MICR VIM	....2.	..2.2..2.....24.....4					
PILE PUM	2...22	.224242222522424422222...2..2...2552.22.....2...22	4.....2.2		.....2.....2..		
POLY CES		..2...2.222..2.2.....2.....2	....2.....2				
POLY CUS		.....2.	552				
POLY VIR		2..2..2.....2.....2					
RUBU SPP		.....2..22.....22.222....222...	.222	.....2....	4...22...4....22	.2.....2..	
RUDB LAC		2.2...222224..22...2...22.2...2.....2..	2				
SIDA HER	2.....	...2.....52242554.....425					
SOLI UNK	2	.....2...222222.....2...4..2...2..22.2422..222...	.2.....2				
TOXI RAD		.2.2..2.....2.....2	..22				
URTI DIO		.....2.....2.....22...	2				
VERB ALT		2222.44.22.5.....522445542555.2.22242..45555555...	22.2.2..2		2	.....2.	
VIOL SOR		2.222542.22222.22224444244424452444.2.22444244222.2					
VITI RIP		.....2.....2....2.....2.2.....2...				.....2..	
OXAL STR	22..22	..2.....2.....2		22	.....2.2		
PHAR ARU		545252.5525.2222..2.....2	5	4555554.44445	.....2...		455.4
SOLI CAN			..4	2.....2	2.....4.....4		
VERN GIG		.....2.....2....	..2	2.....2	2		
BOEH CYL	2...22	22224..2.22.2..22.2.....222.....2	4...22.....2.	54.2..2.24.24	2.22..22222222222	...2	
ARTH HIS			.2.....2	2.....42..2.	2		
ASTE RAC			.222		...22.....5		
CUSC GRO			..2		2.2		
CYPE ODE	.2.22.			2	.....2..2.		
IMPA CAP			..4.2224222252..2	.2	42222222224422222	...2	
GEUM SPP		5	.2.2	2.....2	...2.....2..225		
AGRO PER					.....4.2222..555		
ALIS SUB					.....2.2..2...		...2.
APOC CAN	2.....				.....2.22.....22		
ASCL INC				22	.....2...2		
CARE CRI					....2222.2...2		
CARE LUR					...4.222222..222		
CARE TRI		2..22		55	.....4..22	...2	.2...
CARE VUL				54....4224	.....2242225.422		
CYPE ESC				.....5...4			
CYPE STR				.....4...5		...2	
DIPS SYL					222		
ELEO OVA				.2....42..4	.....22.2..2	...2	
EPIL COL				...2.....2..2	.....2.222.2.2		
GALI TIN	....2.		...2	2..2..4222..2	.2442.2222222.222	..2	2.2..
HIBI MOS				22222	..442.42222222522	...2...22.....2	.2..2
HYPE MUT	....2.		.2	.....2...22	22..2..222222.222	...2	
JUNC EFF				.2...4252..4	2222.2244255.524	...2.....2.	55522
JUNC TEN				2.....222	...2....2522..222	...2	
LEER ORY			...2	.25.22..2222	25555.555.5445242	.....2..	2..45
LUDW ALT				.....222.2.2.	2.....2.....2..		
LUDW PAL				2	..2.22.....22...	...2	2..22
LYCO AME				.....2.2..2	....2.2..2222.2.2		
LYCO COM		..2.2....2..2.22.2	.2		.....22.2222.442	.....2..	
LYSI NUM				25....2564.42	.....2....2..		..2..
MIMU RIN	2				..2....2.2.2..22		
ONOC SEN			.254		52225422224..22.	...2.....2.....2.222	
PENT SED	2....2	.2		.2.....22..22	...2	...2	
POLY COC	22..22				.....4.2....25..		
POLY HYD			2	.....5..	2		2....
POLY PEN			..2	.....2.	256		2
POLY SAG			.22.....55	.2...25444.22	42222.2.2222..22.	...2	
ROSA MUL			...2	.....2....	.2.....222		
SCIR ATR				.....2.2242.	.....2....2..		
ALNU SER	2.....				2	.2.....2..2...2..22	
CEPH OCC	2		...2		...222.....2..2..	...22.22..2	
CORN AMO			.2		.....2.2	.2222.2..2.....2.2....2.	
LEMN MIN			.4	..252	...2.2442.5.25...	22244255554555555555555242	45544
SAUR CER		......4.......4.2				..422242...24	
SPIR POL					......2...2.22...	222424455524555555222522	44222
WOLF COM					.....5...	55555555645555555.555555	55444
SAMPLE	ST	D E F G H L M N U V W C	FJK Q C	X Z A B	K O PX Y	A B C I J	X
		C	C	A B			
			1 1111222	1	11	1	
	212345	1234123123412345123123412345612312341234512345678134	51151470369 25 9 256	4602345234545	3579131234516 8123	123412312312345678234567	12379

Table 3
Summary of the Most Important Herbaceous Layer Species in Each Vegetation Type

	Community						
Species	**Beach**	**Stream-side Forest**	**River Flats**	**New Swale**	**Old Swale**	**Swamp**	**Marsh**
SALI EXI	**10.04**						
AGRO CAP	8.37						
BIDE DIS	8.37						
VIOL SOR		**15.54**					
ELYM VIR		**14.84**					
IMPA PAL		14.43					
LEER VIR			24.33				
IMPA CAP			**14.89**		**9.41**		
LAPO CAN			13.94				
PHAR ARU				**14.53**			**15.79**
POLY SAG				10.42			
LEER ORY				10.18	8.62		**16.71**
BOEH CYL					8.23		
LEMN MIN						34.04	22.66
SPIR POL						34.04	22.66
WOLF COM						32.62	22.66
JUNC EFF							**22.66**

Note: All TWINSPAN indicator species, shown in bold type, are included regardless of their importance value. Values are the three highest importance values based on percentage cover and frequency of occurrence of each species. Species codes are explained in Appendix D.

Communities

The plant communities defined from the ground layer are presented and amended with calculated importance values for the dominant species from all strata.

Beach. Beaches are the exposed sand and mud margins of the river pool. Plots in this vegetation type are dominated along their upslope side by dense colonies of *Salix exigua* shrubs surrounding frequent small *Salix nigra* shrubs and *Amorpha fruticosa*. Other woody river species, such as *Acer saccharinum*

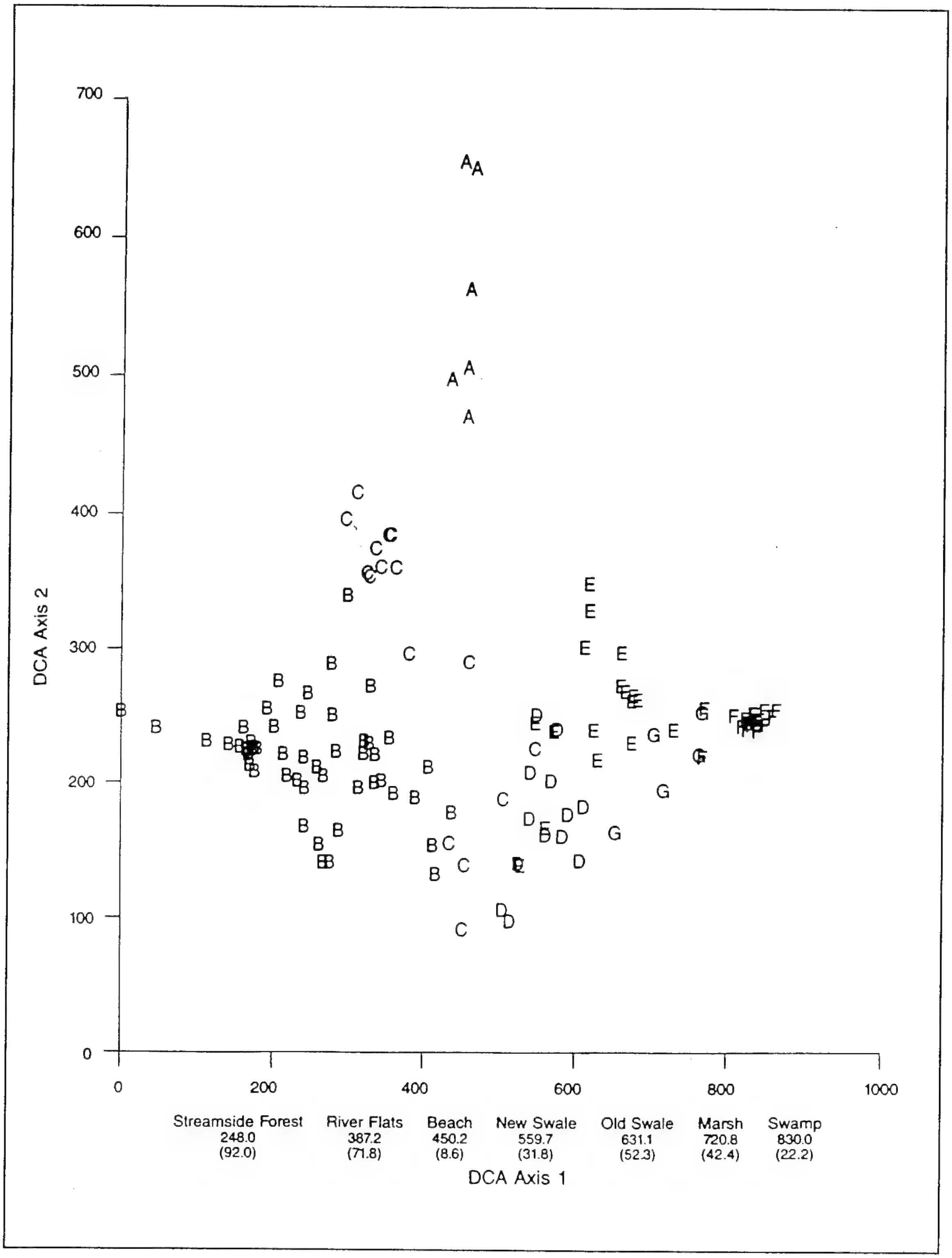

Figure 8. DECORANA ordination of plot data by plant community (Mean scores for axjs 1 are in parentheses. Labels are taken from Table 2. beach (A), streamside forest (B), river flats (C), new swale (D), old swale (E), swamp (F), and marsh (G))

Table 4
Pearson r Correlation Matrix Comparing Directly Measured Environmental Gradients with the First Two DECORANA Axes for 147 Plots

	DCA Axes	
Environmental Variable	**Axis 1**	**Axis 2**
Water depth	0.759	--
Sand	-0.343	0.527
Clay	0.365	-0.507
Silt	0.257	-0.426

Note: Pearson r values are statistically significant at $P < 0.0001$ except for axis 1 × silt, which has $P < 0.005$.

and *Plantanus occidentalis*, also occur as shrubs. Individuals large enough to be classified as trees, with the exception of *S. nigra*, are not found outside the neighboring river flats forest. Tables 5-7 list importance values and their components for herbs, shrubs, and trees in the beach community.

Although defined by its herb layer, no beach community herbaceous species has an importance value greater than 5 percent. Most prominent in this layer is juvenile *S. exigua* with an importance value of 10.04 out of a possible 200. Thirty-two of the remaining taxa have a frequency above 33 percent yet have a low importance value between 8.37 and 2.51. Beaches are ranked fourth among the seven communities in number of species and sixth in number of plots, yet they have the least total cover. This characterizes the community as species rich but individual poor. Indeed, herb layer plot counts often approached 20 species/m^2 with a considerable amount of bare ground included.

Average water depth in beach plots is zero. Frequent, brief flooding and the subsequent short growing season, however, result in vegetation structure that scores third from the dry end of the DCA ordination. The resolution of county soil maps is not fine enough to distinguish between the beach and immediate higher ground, which is mapped as Huntington silt loam, a deep, well-drained, floodplain unit. However, soil texture on the beach is typically 75 to 95 percent sand and should thus be classified as sand to loamy sand to sandy loam.

Streamside forest. The extensive streamside forest is a part of the diminishing bottomland hardwoods community once common along tributary streams and terrace slopes in the Ohio and similar river valleys. Most plots here are under full canopy of *A. saccharinum* and some *A. negundo*. Young *A.saccharinum saplings*, classified as shrubs, are also present in one third of the plots. *Prunus serotina*, *Juglans nigra*, and *Robinia pseudoacacia* are

Table 5
Frequency, Cover, Relative Values, and Importance Values for the Herbaceous Layer in the Beach Community

Species	Frequency	Coverage	Relative Frequency	Relative Coverage	Importance Value
SALI EXI	100.00	15.00	5.00	5.04	10.04
AGRO CAP	83.33	12.50	4.17	4.20	8.37
BIDE DIS	83.33	12.50	4.17	4.20	8.37
AMOR FRU	66.67	10.00	3.33	3.36	6.69
EUPA SER	66.67	10.00	3.33	3.36	6.69
ONOC SEN	66.67	10.00	3.33	3.36	6.69
POLY COC	66.67	10.00	3.33	3.36	6.69
BOEH CYL	50.00	7.50	2.50	2.52	5.02
CYPE ODE	50.00	7.50	2.50	2.52	5.02
ECLI PRO	50.00	7.50	2.50	2.52	5.02
ERAG PEC	50.00	7.50	2.50	2.52	5.02
MOLL VER	50.00	7.50	2.50	2.52	5.02
PILE PUM	50.00	7.50	2.50	2.52	5.02
PLAT OCC	50.00	7.50	2.50	2.52	5.02
RUME VER	50.00	7.50	2.50	2.52	5.02
ACER SAC	33.33	5.00	1.67	1.68	3.35
AMAR SPP	33.33	5.00	1.67	1.68	3.35
APIO AME	33.33	5.00	1.67	1.68	3.35
ARTE VUL	33.33	5.00	1.67	1.68	3.35
CAMP RAD	33.33	5.00	1.67	1.68	3.35
CHEN AMB	33.33	5.00	1.67	1.68	3.35
CYNA LAE	33.33	5.00	1.67	1.68	3.35
ERIG PHI	33.33	5.00	1.67	1.68	3.35
EUPA FIS	33.33	5.00	1.67	1.68	3.35
EUPH HUM	33.33	5.00	1.67	1.68	3.35
LEER VIR	33.33	5.00	1.67	1.68	3.35
PANI CLA	33.33	5.00	1.67	1.68	3.35
PENT SED	33.33	5.00	1.67	1.68	3.35
PLAN RUG	33.33	5.00	1.67	1.68	3.35
SOLA NIG	33.33	5.00	1.67	1.68	3.35
STRO HEL	33.33	5.00	1.67	1.68	3.35
XANT STR	33.33	5.00	1.67	1.68	3.35
AMPH BRA	33.33	2.50	1.67	0.84	2.51
Other taxa (28)	466.67	70.00	23.33	23.53	46.86
Total	2,000	297.50	100.00	100.00	200.00

Table 6
Frequency, Density, Relative Values, and Importance Values for the Shrub Layer in the Beach Community

Species	Frequency	Density	Relative Frequency	Relative Density	Importance Value
SALI EXI	83.33	224	25.00	73.68	98.68
SALI NIG	66.67	30	20.00	9.87	29.87
AMOR FRU	66.67	20	20.00	6.58	26.58
ACER SAC	66.67	9	20.00	2.96	22.96
PLAT OCC	16.67	13	5.00	4.28	9.28
CORN AMO	16.67	6	5.00	1.97	6.97
POPU DEL	16.67	2	5.00	0.66	5.66
Total	333.33	304	100.00	100.00	200.00

Table 7
Frequency, Density, Relative Values, Basal Area, and Importance Values for Trees in the Beach Community

Species	Basal Area	Frequency	Density	Relative Basal Area	Relative Frequency	Relative Density	Importance Value
SALI NIG	9.88	33.33	2	100.00	100.00	100.00	300.00
Total	9.88	33.33	2	100.00	100.00	100.00	300.00

usually found in the higher margins of creekside or riverside plots. This community type is richest in number of woody species (20). Tables 8-10 list importance values and their components for herbs, shrubs, and trees in the streamside forest.

The herbaceous layer is characterized by several frequent, high cover species: *Viola sororia* has the highest importance value but can hardly be called dominant as it is found in the lowest layer, growing in the dense shade of other herbs. It is notable for its frequency (88 percent) and fidelity to this vegetation type. *Elymus virginicus, Impatiens pallida,* and *Pilea pumila* are of comparable frequency and importance. *Laportea canadensis* and *Verbesina alternifolia* are often encountered as robust, pure, dominant herb layers. *Arundinaria gigantea*, uneven in distribution, is quite apparent as dense thickets in bends of the stream draining the swamp.

Similar to the beach community, streamside forest plots had 0 cm average water depth. However, hydrology reflected by species composition ranks this community as the driest on the site. Most of the plots are on Chagrin-Melvin

Table 8
Frequency, Cover, Relative Values, and Importance Values for the Herbaceous Layer in the Streamside Forest Community

Species	Frequency	Coverage	Relative Frequency	Relative Coverage	Importance Value
VIOL SOR	88.46	293.50	7.57	7.97	15.54
ELYM VIR	82.69	286.00	7.07	7.77	14.84
IMPA PAL	63.46	331.50	5.43	9.00	14.43
PILE PUM	61.54	258.50	5.26	7.02	12.28
GLEC HED	42.31	316.50	3.62	8.59	12.21
LAPO CAN	42.31	304.00	3.62	8.25	11.87
LEER VIR	32.69	291.50	2.80	7.92	10.71
AMPH BRA	69.23	173.00	5.92	4.70	10.62
VERB ALT	67.31	87.50	5.76	2.38	8.13
BOEH CYL	30.77	135.50	2.63	3.68	6.31
CRYP CAN	38.46	50.00	3.29	1.36	4.65
SOLI GIG	38.46	50.00	3.29	1.36	4.65
POLY CES	17.31	105.50	1.48	2.86	4.34
GALI APA	32.69	42.50	2.80	1.15	3.95
PHAR ARU	30.77	40.00	2.63	1.09	3.72
RUDB LAC	30.77	40.00	2.63	1.09	3.72
Other taxa (57)	400.00	877.35	34.21	23.82	58.03
Total	1,169.23	3,682.85	100.00	100.00	200.00

Table 9
Frequency, Density, Relative Values, and Importance Values for the Shrub Layer in the Streamside Forest Community

Species	Frequency	Density	Relative Frequency	Relative Density	Importance Value
ACER SAC	32.69	109	32.69	41.76	74.45
ROBI PSE	19.23	48	19.23	18.39	37.62
ACER NEG	15.38	34	15.38	13.03	28.41
FRAX PEN	7.69	35	7.69	13.41	21.10
CORN AMO	3.85	18	3.85	6.90	10.74
JUGL NIG	5.77	3	5.77	1.15	6.92
SAMB CAN	3.85	5	3.85	1.92	5.76
CARY COR	3.85	4	3.85	1.53	5.38
CEPH OCC	3.85	2	3.85	0.77	4.61
CELT OCC	1.92	2	1.92	0.77	2.69
CARY LAC	1.92	1	1.92	0.38	2.31
Total	100.00	261	100.00	100.00	200.00

Table 10
Frequency, Density, Basal Area, Relative Values, and Importance Values for the Tree Layer in the Streamside Forest Community

Species	Basal Area	Frequency	Density	Relative Basal Area	Relative Frequency	Relative Density	Importance Value
ACER SAC	1,505.27	69.23	182	70.00	36.73	60.47	167.90
ACER NEG	192.02	21.15	43	9.02	11.22	14.29	34.53
ROBI PSE	118.61	21.15	22	5.57	11.22	7.31	24.10
ACER SAD	62.53	25.00	18	2.94	13.27	5.98	22.18
JUGL NIG	96.36	21.15	17	4.53	11.22	5.65	21.40
PLAT OCC	99.03	5.77	4	4.65	3.06	1.33	9.04
ULMU AME	8.00	5.77	4	0.38	3.06	1.33	4.77
PRUN SER	12.68	5.77	3	0.60	3.06	1.00	4.65
FRAX PEN	17.88	3.85	2	0.84	2.04	0.66	3.55
SALI NID	5.80	3.85	2	0.27	2.04	0.66	2.98
ACER NED	2.65	1.92	2	0.12	1.02	0.66	1.81
SALI NIG	5.94	1.92	1	0.28	1.02	0.33	1.63
JUGL NID	2.24	1.92	1	0.11	1.02	0.33	1.46
Total	2,129.01	188.46	301	100.00	100.00	100.00	300.00

silt loams with some Huntington soils. This soil unit is characterized as a deep, mostly well-drained floodplain soil common to river tributaries.

River flats. River flats make up the remainder of extant bottomland hardwood forests. This community is characterized by high basal area of *A. saccharinum* and *Populus deltoides* individuals on frequently flooded mud and sandbars. Shrubs, the most important being *A. saccharinum* saplings, are less important here than in the higher streamside forest. Large *P. deltoides* emerge from bare mud and bow low over the water where this community type extends the river's edge. River flats are usually found on river islands or low-lying extensions below the river berm. Tables 11-13 list importance values and their components for herbs, shrubs, and trees.

While the lowest areas of this community are often bare, most plots show greater than 100 percent cover. *Leersia virginica, I. capensis,* and *Laportea canadensis* are most important among the herbs, followed by *Boehmeria cylindrica, Polygonum saggitatum,* and *I. pallida.* Although species richness is high among the Green Bottom communities, total frequency is fairly low, surpassing only the permanently inundated swamp and marsh communities. This calculation supports the casual observation that many river flats species are found in almost pure "patches" of infrequent occurrence.

Table 11
Frequency, Cover, Relative Values, and Importance Values for the Herbaceous Layer in the River Flats Community

Species	Frequency	Coverage	Relative Frequency	Relative Coverage	Importance Value
LEER VIR	82.35	309.00	11.11	13.22	24.33
IMPA CAP	70.59	125.50	9.52	5.37	14.89
LAPO CAN	41.18	196.00	5.56	8.38	13.94
BOEH CYL	29.41	191.00	3.97	8.17	12.14
POLY SAG	23.53	201.00	3.17	8.60	11.77
IMPA PAL	23.53	188.50	3.17	8.06	11.24
PILE PUM	17.65	186.00	2.38	7.96	10.34
SICY ANG	11.76	183.50	1.59	7.85	9.44
APIO AME	17.65	103.00	2.38	4.41	6.79
ARTH HIS	11.76	100.50	1.59	4.30	5.89
POLY CES	11.76	100.50	1.59	4.30	5.89
PHYT AME	5.88	98.00	0.79	4.19	4.99
POLY HYD	5.88	98.00	0.79	4.19	4.99
AMPH BRA	29.41	21.60	3.97	0.92	4.89
VERB ALT	29.41	12.50	3.97	0.53	4.50
Other taxa (39)	329.41	223.00	44.44	9.54	53.98
Total	741.18	2,337.60	100.00	100.00	200.00

Table 12
Frequency, Density, Relative Values, and Importance Values for the Shrub Layer in the River Flats Community

Species	Frequency	Density	Relative Frequency	Relative Density	Importance Value
ACER SAC	29.41	17	35.71	25.76	61.47
ALNU SER	5.88	19	7.14	28.79	35.93
CORN AMO	11.76	12	14.29	18.18	32.47
ACER NEG	17.65	4	21.43	6.06	27.49
LIND BEN	5.88	11	7.14	16.67	23.81
CEPH OCC	5.88	2	7.14	3.03	10.17
FRAX PEN	5.88	1	7.14	1.52	8.66
Total	82.35	66	100.00	100.00	200.00

Table 13
Frequency, Density, Basal Area, Relative Values, and Importance Values for the Tree Layer in the River Flats Community

Species	Basal Area	Frequency	Density	Relative Basal Area	Relative Frequency	Relative Density	Importance Value
ACER SAC	385.82	82.35	56	61.65	42.42	65.88	169.96
POPU DEL	136.11	35.29	9	21.75	18.18	10.59	50.52
SALI NID	26.44	11.76	7	4.23	6.06	8.24	18.52
ACER SAD	23.20	17.65	2	3.71	9.09	2.35	15.15
SALI NIG	32.27	11.76	3	5.16	6.06	3.53	14.75
PLAT OCC	7.68	5.88	2	1.23	3.03	2.35	6.61
ACER NED	3.94	5.88	2	0.63	3.03	2.35	6.01
ACER NEG	6.25	5.88	1	1.00	3.03	1.18	5.20
FRAX AME	1.65	5.88	1	0.26	3.03	1.18	4.47
ULMU AME	1.29	5.88	1	0.21	3.03	1.18	4.41
FRAX PEN	1.13	5.88	1	0.18	3.03	1.18	4.39
Total	625.77	194.12	85	100.00	100.00	100.00	300.00

Species composition ranks the river flats community second to the driest, besides the streamside forest. Average water depth in the plots is 0 cm, but flooding is frequent and often prolonged. The soils are mapped as either Huntington or Chagrin-Melvin silt loams. Each is described above as a low floodplain unit.

New swale. These are wet old fields with normally inundated central drains, or "swales," dominated by obligate wetland species. *Fraxinus pennsylvanica* shrubs are the most common woody taxon. Only 25 stems were recorded for trees and shrubs combined in 13 new swale plots, giving this the lowest density of woody plants for any community except the marsh. Tables 14-16 list importance values and their components for herbs, shrubs and trees in the new swale community.

The herbaceous layer resembles a grassy wet meadow dominated by *Phalaris arundinacea, P. sagittatum,* and *L. oryzoides*. *Boehmeria cylindrica* and *Lysimachia nummilaria* complete the list of those species occurring in at least two thirds of the plots. The herb layer in this and the old swale form a mosaic; bands of a few species with unusually high cover often run parallel to drains or concentrate in depressions. This community has the greatest number of species from the Poaceae and Cyperaceae families. Total frequency and cover are high, describing a tangled mat of herbs.

Table 14
Frequency, Cover, Relative Values, and Importance Values for the Herbaceous Layer in the New Swale Community

Species	Frequency	Coverage	Relative Frequency	Relative Coverage	Importance Value
PHAR ARU	92.31	322.50	7.95	6.58	14.53
POLY SAG	61.54	251.00	5.30	5.12	10.42
LEER ORY	61.54	239.00	5.30	4.88	10.18
BOEH CYL	61.54	238.00	5.30	4.86	10.16
LYSI NUM	61.54	238.00	5.30	4.86	10.16
GALI TIN	53.85	188.00	4.64	3.84	8.47
JUNC EFF	46.15	208.00	3.97	4.25	8.22
PENT SED	38.46	217.50	3.31	4.44	7.75
SCIR ATR	38.46	192.50	3.31	3.93	7.24
LUDW ALT	38.46	170.00	3.31	3.47	6.78
CARE VUL	46.15	112.00	3.97	2.29	6.26
ELEO OVA	30.77	154.50	2.65	3.15	5.80
HYPE MUT	23.08	164.00	1.99	3.35	5.34
ARTH HIS	30.77	119.00	2.65	2.43	5.08
JUNC TEN	30.77	116.50	2.65	2.38	5.03
EPIL COL	23.08	116.50	1.99	2.38	4.37
LYCO AME	23.08	116.50	1.99	2.38	4.37
HIBI MOS	38.46	51.50	3.31	1.05	4.36
Other taxa (30)	361.54	1683.00	31.13	34.36	65.49
Total	1,161.54	4,898.00	100.00	100.00	200.00

Table 15
Frequency, Density, Relative Values, and Importance Values for the Shrub Layer in the New Swale Community

Species	Frequency	Density	Relative Frequency	Relative Density	Importance Value
FRAX PEN	30.77	16	36.36	69.57	105.93
CEPH OCC	15.38	2	18.18	8.70	26.88
ULMU AME	15.38	2	18.18	8.70	26.88
CORN AMO	7.69	1	9.09	4.35	13.44
GLED TRI	7.69	1	9.09	4.35	13.44
SALI NIG	7.69	1	9.09	4.35	13.44
Total	84.62	23	100.00	100.00	200.00

Table 16
Frequency, Density, Basal Area, Relative Values, and Importance Values for the Tree Layer in the New Swale Community

Species	Basal Area	Frequency	Density	Relative Basal Area	Relative Frequency	Relative Density	Importance Value
ACER SAC	28.27	7.69	1	60.09	50.00	50.00	160.09
FRAX PEN	18.78	7.69	1	39.91	50.00	50.00	139.91
Total	47.05	15.38	2	100.00	100.00	100.00	300.00

New swale vegetation is in standing water much of the year. Average plot water depth in September 1992 was 13.9 cm, with a standard deviation of equivalent magnitude (12.7 cm). This is slightly deeper than the old swale, but the new swale community ranks slightly drier, with a position fourth from the left along DCA axis 1 (Figure 8). Soils are the Lindside and Melville silt loams commonly found in wet floodplain hay pastures. These units are deep, with clayey, gray mottled substrata. Much of the new swale community is being flooded by wetland construction. See Gilliam (1991) for a reference to current research on pre- and post-impoundment oxidation-reduction levels in these soils.

Old swale. Old swales are most easily distinguished from new swales by the increased presence of *Cornus ammomum* and *Cephalanthus occidentalis*, two species that require a longer site history of flooded conditions. Seventy-two stems of *C. occidentalis* alone are distributed among half of the 17 old swale plots. Aerial photographs of GBWMA attest to the more recent agricultural use of new swale fields. Tables 17-19 list importance values and their components for old swale herbs, shrubs, and trees.

The quantitative structure of the old swale herb layer suggests a dense variation of the beach community. No species attains 5 percent of the total importance value; 25 species are present in more than one third of the plots. Species richness reaches 20 taxa/m^2. Unlike the beach, total cover per plot is greater than 100 percent. Important species include *I. capensis, L. oryzoides, B. cylindrica,* and *Hibiscus moscheutos.*

Average water depth at sample points was 3.2 cm in July and September 1992. The old swale scores to the dry side of only the swamp and the marsh in ordination space. The same soil units are mapped for both new and old swales.

Swamp. Permanently inundated areas with a full to loose or punctuated woody canopy were classified as swamps. At GBWMA this classification is largely confined to a single, contiguous area known as the "New Swamp" because of its rapid expansion. This is the only vegetation type with more

Table 17
Frequency, Cover, Relative Values, and Importance Values for the Herbaceous Layer in the Old Swale Community

Species	Frequency	Coverage	Relative Frequency	Relative Coverage	Importance Value
IMPA CAP	100.00	107.50	4.93	4.49	9.41
LEER ORY	88.24	102.50	4.35	4.28	8.62
BOEH CYL	82.35	100.00	4.06	4.17	8.23
HIBI MOS	82.35	100.00	4.06	4.17	8.23
GALI TIN	82.35	87.00	4.06	3.63	7.69
JUNC EFF	82.35	74.00	4.06	3.09	7.15
HYPE MUT	70.59	82.00	3.48	3.42	6.90
ONOC SEN	82.35	61.00	4.06	2.55	6.60
CARE VUL	52.82	77.00	2.90	3.21	6.11
POLY SAG	70.59	56.00	3.48	2.34	5.82
LYCO COM	52.94	74.50	2.61	3.11	5.72
CARE LUR	58.82	64.00	2.90	2.67	5.57
AGRO PER	47.06	59.00	2.32	2.46	4.78
JUNC TEN	47.06	59.00	2.32	2.46	4.78
LYCO AME	47.06	59.00	2.32	2.46	4.78
LEMN MIN	47.06	46.00	2.32	1.92	4.24
EPIL COL	35.29	54.00	1.74	2.25	3.99
GEUM SPP	29.41	51.50	1.45	2.15	3.60
MIMU RIN	35.29	41.00	1.74	1.71	3.45
ROTA RAM	35.29	41.00	1.74	1.71	3.45
ROSA MUL	23.53	49.00	1.16	2.04	3.20
APOC CAN	29.41	38.50	1.45	1.61	3.06
LUDW PAL	29.41	38.50	1.45	1.61	3.06
CARE CRI	35.29	28.00	1.74	1.17	2.91
Other taxa (67)	676.47	846.50	33.33	35.32	68.66
Total	2,029.41	2,396.50	100.00	100.00	200.00

woody (ten live, seven dead) than herbaceous (seven) taxa observed. The effects of longer term inundation are obvious in the community. Live, dense *A. saccharinum* and *S. nigra* canopy, with *C. ammomum* understory, grades with increasing water depth and permanence to a thinner overstory of dead

Table 18
Frequency, Density, Relative Values, and Importance Values for the Shrub Layer in the Old Swale Community

Species	Frequency	Density	Relative Frequency	Relative Density	Importance Value
CEPH OCC	47.06	72	44.44	52.55	97.00
CORN AMO	5.88	51	5.56	37.23	42.78
ALNU SER	17.65	6	16.67	4.38	21.05
ACER SAC	11.76	4	11.11	2.92	14.03
ACER NEG	11.76	2	11.11	1.46	12.57
NYSS SYL	5.88	1	5.56	0.73	6.29
SALI NIG	5.88	1	5.56	0.73	6.29
Total	105.88	137	100.00	100.00	200.00

Table 19
Frequency, Density, Basal Area, Relative Values, and Importance Values for the Tree Layer in the Old Swale Community

Species	Basal Area	Frequency	Density	Relative Basal Area	Relative Frequency	Relative Density	Importance Value
ACER SAC	8.61	11.76	6	38.99	40.00	60.00	138.99
SALI NIG	9.63	5.88	2	43.61	20.00	20.00	83.61
ULMU AME	2.19	5.88	1	9.92	20.00	10.00	39.92
SALI NID	1.65	5.88	1	7.48	20.00	10.00	37.48
Total	22.08	29.41	10	100.00	100.00	100.00	300.00

individuals. *Cephalanthus occidentalis* dominates the deepest, wettest, central areas, resembling the central portion of the oldest swamp on the site (Liu 1991). Live *S. nigra* line both sides of the 1.5- to 2-m-deep drain bisecting the New Swamp (see landmarks, Appendix C). *Alnus serrulata* also occurs in more than half of the surveyed region, often forming imposing thickets with *C. amomum*. Tables 20-22 list importance values and their components for herbs, shrubs, and trees in the swamp community.

Lemna minor, spirodela polyrhiza, and two *Wolffia* species, all nonrooted, floating herb species, are present at greater than 50 percent cover in all plots. The *Wolffia* taxa, *W. columbiana* and *W. papulifera,* are always present together in a ratio of less than 1:100. No *W. punctata* was recorded. It is believed that this specific epithet is commonly applied in error to the above combination. *Saururus cernuus* was the only other herbaceous species

Table 20
Frequency, Cover, Relative Values, and Importance Values for the Herbaceous Layer in the Swamp Community

Species	Frequency	Coverage	Relative Frequency	Relative Coverage	Importance Value
LEMN MIN	100.00	60.00	17.02	17.02	34.04
SPIR POL	100.00	60.00	17.02	17.02	34.04
WOLF COM	95.83	57.50	16.31	16.31	32.62
CORN AMO	37.50	22.50	6.38	6.38	12.77
SAUR CER	33.33	20.00	5.67	5.67	11.35
ALNU SER	25.00	15.00	4.26	4.26	8.51
ONOC SEN	25.00	15.00	4.26	4.26	8.51
Other taxa (29)	170.83	102.50	29.08	29.08	58.16
Total	587.50	352.50	100.00	100.00	200.00

Table 21
Frequency, Density, Relative Values, and Importance Values for the Shrub Layer in the Swamp Community

Species	Frequency	Density	Relative Frequency	Relative Density	Importance Value
CORN AMO	100.00	335	31.17	47.12	78.29
CEPH OCC	75.00	164	23.38	23.07	46.44
ALNU SER	54.17	155	16.88	21.80	38.68
ACER SAC	33.33	31	10.39	4.36	14.75
SALI NIG	25.00	10	7.79	1.41	9.20
FRAX PEN	20.83	13	6.49	1.83	8.32
PLAT OCC	8.33	2	2.60	0.28	2.88
ULMU AME	4.17	1	1.30	0.14	1.44
Total	320.83	711	100.00	100.00	200.00

recorded that requires permanent inundation. Several obligate emergent species were recorded by other researchers in the old swamp (not surveyed in this work) and are included in Appendix D.

Water depth in the new swamp averaged 41.3 cm over all plots. Species composition resulted in this vegetation type being scored the wettest along DCA axis 1. Soils are classified as Melvin silt loams.

Table 22
Frequency, Density, Basal Area, Relative Values, and Importance Values for the Tree Layer in the Swamp Community

Species	Basal Area	Frequency	Density	Relative Basal Area	Relative Frequency	Relative Density	Importance Value
ACER SAD	77.47	50.00	40	20.49	20.69	25.16	66.34
ACER SAC	71.73	33.33	36	18.97	13.79	22.64	55.41
SALI NIG	66.37	25.00	24	17.56	10.34	15.09	43.00
PLAT OCD	63.80	29.17	14	16.88	12.07	8.81	37.75
ACER NED	20.55	25.00	12	5.44	10.34	7.55	23.33
PLAT OCC	29.58	20.83	7	7.82	8.62	4.40	20.85
ULMU AMD	8.95	12.50	5	2.37	5.17	3.14	10.68
FRAX PEN	10.35	8.33	7	2.74	3.45	4.40	10.59
SALI NID	9.04	8.33	4	2.39	3.45	2.52	8.36
POPU DED	7.29	4.17	3	1.93	1.72	1.89	5.54
ULMU AME	1.80	8.33	2	0.48	3.45	1.26	5.18
ACER NEG	6.76	4.17	2	1.79	1.72	1.26	4.77
PYRU SPP	1.89	4.17	1	0.50	1.72	0.63	2.85
TILI AMD	1.45	4.17	1	0.38	1.72	0.63	2.74
GLED TRI	0.99	4.17	1	0.26	1.72	0.63	2.61
Total	378.02	241.67	159	100.00	100.00	100.00	300.00

Marsh. Permanently inundated areas of emergent vegetation with little or no woody component are classified as marshes. Table 23 summarizes frequency, cover, and importance values for the dominant herbaceous species in the marsh community. *Lemna minor, S. polyrhiza,* and the two *Wolffia* species have the highest presence, along with *Juncus effusus,* the morphologically dominant herb. *Phalaris arundinacea* is the only other taxon present in at least 30 percent of the plots. Open water is common, as cover averaged less than 67 percent over all sample points. Wet meadows were included in this classification when drawing the vegetation map. This second type of marsh is usually close to monocultural and often dominated by *P. arundinacea.*

The marsh community is often poorly defined physiographically. Plots laid in the marsh just north of the Jenkins House (Homestead--Appendix C) were divided by the classification procedure between marsh, new swale, and old swale. Drier site species take advantage of changes in hydrology more readily than would be possible under the swamp canopy. Average water depth in the marsh plots was 25.0 cm in August but was often 0 cm or 50 cm depending on the precise location. Lindside silt loam is found under the marsh and wet meadow sites.

Table 23
Frequency, Cover, Relative Values, and Importance Values for the Herbaceous Layer in the Marsh Community

Species	Frequency	Coverage	Relative Frequency	Relative Coverage	Importance Value
JUNC EFF	38.46	38.50	11.11	11.54	22.66
LEMN MIN	38.46	38.50	11.11	11.54	22.66
SPIR POL	38.46	38.50	11.11	11.54	22.66
WOLF COM	38.46	38.50	11.11	11.54	22.66
LEER ORY	23.08	33.50	6.67	10.04	16.71
LUDW PAL	23.08	33.50	6.67	10.04	16.71
PHAR ARU	30.77	23.00	8.89	6.90	15.79
Other taxa (12)	115.38	89.50	33.33	26.84	60.17
Total	346.15	333.50	100.00	100.00	200.00

Discussion

Gilliam and Turrill (1993) noted that few vegetation studies have analyzed gradient interaction with the herb layer. Their work pointed out the usefulness of this approach in montane eastern deciduous forests. Such a focus is all the more important in wetland-dominated regions where the only well-developed layer of many "stands" is herbaceous. TWINSPAN classification of GBWMA vegetation, considering only the herb layer, defined communities that were both identifiable in the field and along ordination axes correlated to hydrology and soil texture. Clustering of plots by floristic similarity (discussed in the next chapter and including taxa from all strata) reinforces the same classification of sample points.

Attempts at definition of vegetation types through classification of either woody stratum produced clusters that were difficult to interpret. Woody species do serve as indicators of defined communities. As discussed above, they indicate the relative successional status of wet, old fields and swamps. Their presence may also be misleading; the northeast extension of the New Swamp area at GBWMA (transect K, Appendix C) appears to be part of the ever-expanding deepwater swamp. This area experiences an annual drawdown; thus, increased but irregular woodiness can be taken as an indicator of succession toward the swamp community. This suggests that, in the case of GBWMA wetlands, the herbaceous layer is the least, not the most, plastic stratum.

Similarly, some herb plots under river flats canopy were classified as streamside forest and vice-versa. This seems to indicate a distinction between the two based largely on elevation controlled hydrology--only high river flats

plots were included in the drier streamside forest definition. Comparable is the grading of marsh plots to drier new and old swales discussed in the marsh community section. Herb layer vegetation appears to be the most discerning indicator of environmental conditions in riparian wetlands.

Plant community composition at GBWMA is mainly a response to water presence. Although three of the seven communities recognized were assigned the same value (0) along a water depth gradient, the broad spreading of mean community plot values along the DCA axis strongly correlated to this gradient supports an interpretation based on hydrology. Degree and period of inundation are most accurately integrated by the plants themselves.

Strong negative relationships between sand and clay content in mineral soils have been observed at varying elevations in the eastern coastal plain (Gilliam, Yurish, and Goodwin 1993). A similar relationship exists at GBWMA. Plot samples varied widely in sand and clay content; sand values ranged from 0 to 95 percent, and clay from 5 to 49 percent. However, mean scores for seven of the eight communities fell within a 131-point range along the 641-point ordination axis correlated to the texture gradient. With the exception of the obvious extreme of the sandy beach community, soil texture is seen as a poor indicator of vegetation type at this site.

Flora

GBWMA flora consists of 335 species (one in two forms) belonging to 222 genera in 81 families. Three of these families belong to two divisions of fern and fern allies. Twenty-seven woody taxa are distributed among the seven plant communities as shown in Table 24. Only the marsh community is comprised of a single (herbaceous) stratum.

Table 24
Woody Species Distribution in each Plant Community

Beach	S. side Forest	River Flats	New Swale	Old Swale	Swamp	Marsh	Site Total
8	20	12	8	9	10	0	27
(9.6)	(19.6)	(16.2)	(8.0)	(9.3)	(17.0)	(0.0)	(9.3)

Note: Percentages of the community total are indicated by parentheses.

Species from the Asteraceae (46 species, 13.8 percent of total), Poaceae (43, 12.9 percent), and Cyperaceae (23, 6.9 percent) account for one third of all taxa recorded on the site. Figure 9 compares species counts from these major families to the total number of species found in each of the plant communities. Forty-six taxa (named in the catalogue), yet found outside of the

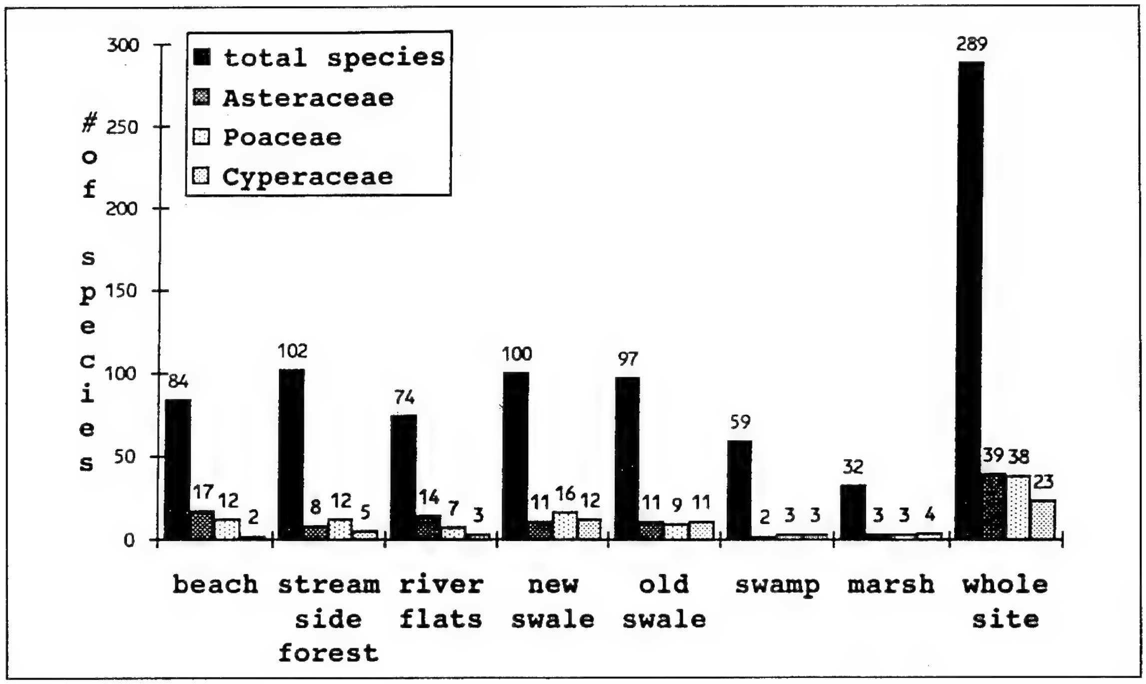

Figure 9. Species totals in each community for the three principal families of GBWMA flora (Taxa found exclusively in disturbed areas were not considered in the site totals)

mapped communities, are not included in the site total category. This "disturbed area" flora is found along fencerows, beside farm roads, and in recently mowed or cultivated fields. It is not considered a percentage of the flora found within the quantitatively determined vegetation types and is excluded from further discussion of the flora except where noted.

Several species of concern in West Virginia are found at GBWMA. Table 25 lists 10 taxa currently considered threatened or endangered by the State Natural Heritage Program. At least one listed taxon was found in each plant community. Three S1 taxa, *Ampelopsis cordata, Carex projecta,* and *Lythrum alatum,* were recorded in the old swale community. *Spermacoce glabra, Amorpha fruticosa,* and *Cyperus squarrosus* were all found along the beach. *Spermacoce glabra* was recorded once previously in a nearby, similar habitat (MUHW) but has not been recorded with the state. *Wolffia columbiana* was discussed in the vegetation section of this chapter. Pending additional investigation of herbaria and in the field, it is reported as a threatened species. No Federally listed species were found.

The vast majority (79.9 percent) of the flora is native. Figure 10 shows that the swamp community has the highest percentage of native taxa (96.6 percent), whereas the community with the least affinity to local species, the beach, is still strongly native (79.5 percent). The site as a whole has 79.9 percent native species, 14.9 percent exotics, and 5.2 percent introduced or adventive native North American (north of Mexico) species. A single specimen of *Morus alba,* found in the streamside forest community, was the only woody

Table 25 Species of Concern Because of Rarity in West Virginia	
Taxon	**Status**
Ampelopsis cordata Michx. - raccoon-grape	S1
Carex projecta Mackenzie - a sedge	S1
Eleocharis palustris L. - a spikerush	S1
Lythrum alatum Pursh - wing-angled loosestrife	S1
Spermacoce glabra Michx. - buttonweed	S1
Wolffia columbiana Karsten - a water-meal	S1
Ammania coccinea Rottb. - toothcup	S2
Amorpha fruticosa - false indigo	S2
Cyperus squarrosus L. - a flatsedge	S2
Eleocharis compressa Sullivant - a spikerush	S2
Note: As defined by the natural heritage program, S1 species are recorded from five or fewer populations in the state, S2 species from 6-20 populations.	

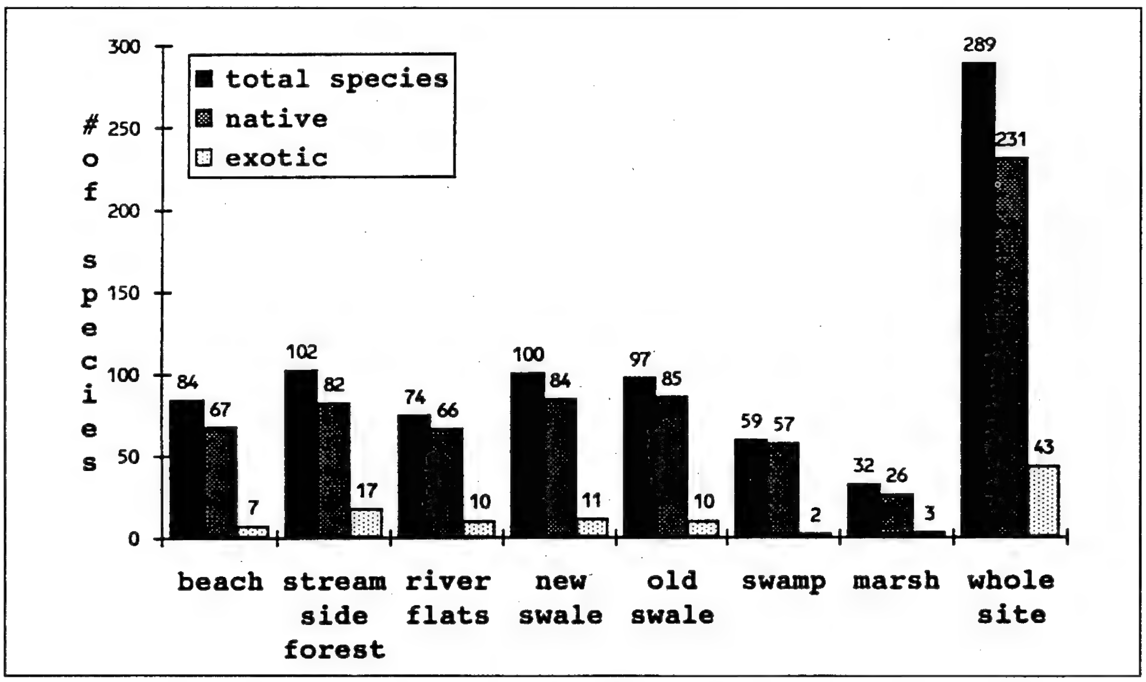

Figure 10. Summary of species geographical affinity within the seven plant communities comprising GBWMA flora (Numbers of taxa found exclusively in disturbed areas have been removed from totals category. The difference between the first and the sum of the last two columns under each community heading is the number of introduced or adventive native North American taxa)

taxon not native to the state. By contrast, disturbed area species (46 taxa, not included in the figure) proved to be mostly exotics (63 percent).

All GBWMA communities meet the U.S. Department of the Army vegetational composition criterion (Environmental Laboratory 1987) for definition as Federal wetlands (fulfillment of soil and hydrological criteria not evaluated). This requirement states that at least half of the species in a stand must be from the three wettest categories of Federally listed plants, namely obligate (found in wetlands 99+ percent of the time), facultative-wet (found in wetlands 67 to 99 percent of the time), and facultative (found in wetlands 34 to 66 percent of the time) wetland species. Figure 11 shows that almost half (46.7 percent) of GBWMA flora is comprised of species from just the first two categories. This high percentage of wetland preferential taxa supports the definition of Green Bottom as a well-established wetland. Twenty-nine (90.6 percent) of the 32 marsh community herbs are wetland preferential species, followed by 74.6 percent of all swamp species. The new and old swale communities are made up of more than 50 percent wetland preferentials, and the community with the lowest percentage, the streamside forest, still has greater than one third (38.6 percent) of its species classified as wetland preferentials. The streamside forest was also the only community to have less than one half of its woody members classified as wetland preferring species.

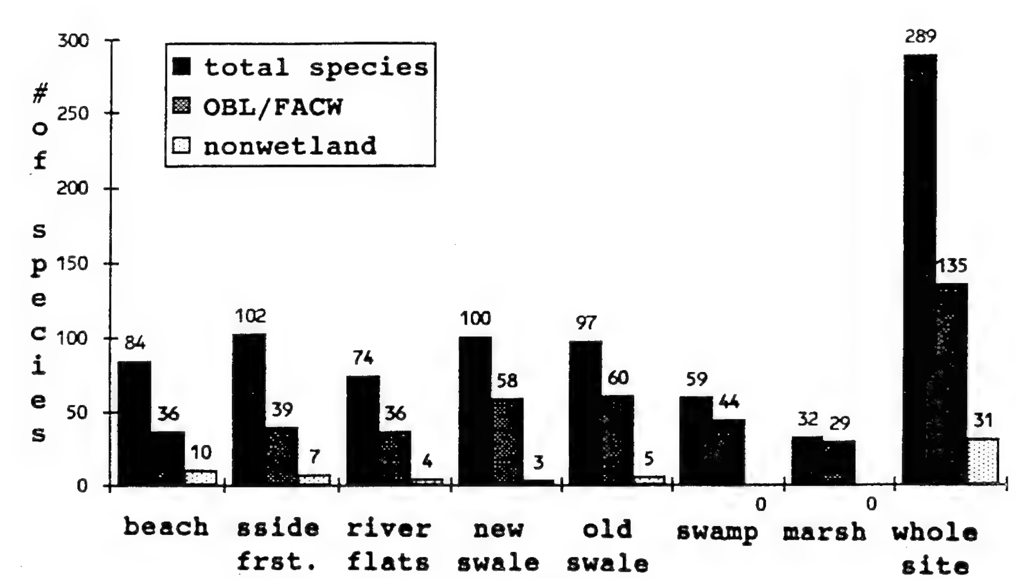

Figure 11. Summary of wetland species in the seven plant communities of GBWMA flora (The numbers of taxa found exclusively in disturbed areas have been removed from the totals column. Occasional wetland species make up the difference between the first and the sum of the last two columns under each community heading. An explanation of all FWS categories can be found in the instructions to the annotated catalogue on file at WES)

The floristic comparison of communities is presented in Table 26. The new and old swale types are most similar (0.574), followed by the river flats and the old swale (0.426), and the river flats and the streamside forest (0.414). Most other communities had less than a third of their species in common.

Table 26
Sorensen's Coefficient of Similarity for the Seven GBWMA Plant Communities

	Beach	S. Side Forest	River Flats	New Swale	Old Swale	Swamp	Marsh
Beach	1.000						
S. Forest	0.261	1.000					
R. Flats	0.295	0.414	1.000				
New Swale	0.165	0.180	0.267	1.000			
Old Swale	0.302	0.234	0.426	0.574	1.000		
Swamp	0.227	0.252	0.321	0.344	0.273	1.000	
Marsh	0.088	0.076	0.173	0.231	0.362	0.157	1.000

The combination of similarity coefficients by unweighted averaging is represented in Table 26. The communities are arranged in the same order as the TWINSPAN classification to facilitate comparison of the two clustering techniques. As predicted by the coefficients in Table 26, the joining of most communities is at a common and low level of similarity.

The GBWMA flora was also compared as a whole to floras from two other Ohio River Valley studies: Ely (1992), a survey of river embayments; and Furry (1978), a survey of riparian "frontal forests." Computation of Sorensen's coefficient of similarity (Table 27) shows that the mostly wetland embayment flora is highly similar to that of the GBWMA site. Even the more limited frontal forest flora shares greater than one half of its specific taxa with Green Bottom. The comparisons are crude, as each of the other studies included only a subset of GBWMA vegetation types.

Table 27
Sorensen's Coefficient of Similarity Comparison of the GBWMA Flora to Two Other Ohio River Floras

Flora Studied	Similarity
Green Bottom	1.000
Ely (embayments)	0.653
Furry (frontal forests)	0.579

Note: GBWMA disturbed area species are not included.

Community similarity. The highly native, wetland characteristic of all plant communities, combined with their low floristic similarity, demonstrates the significance of the site as a whole. The flora indicates seven distinct and undisturbed small-area habitats in close proximity. Clustering of the Sorensen's coefficients at a common, low level supports the conclusion that the community definitions serve as real and consistent distinctions, all on roughly the same level, applicable to field and management decisions.

The order of clustering is also worth noting. Unweighted pair averaging is an agglomerative technique similar to many used in vegetation classification. Although the ordering of samples along the base of the final dendrogram does not have statistical significance (unlike TWINSPAN, the vertical axes may be rotated), the hierarchy to which samples are joined does indicate the relative similarity of each community to the site as a whole. Thus, the two forested, seasonally inundated communities (streamside forest and river flats) are seen floristically as a subset, more like each other than like the rest of the site. They share not only certain aspects of physiography and hydrology but also waterborne seeds traveling to and from the river.

The two clustered, wet, old field types and the new and old swales also share physiography and hydrology. They have little connection with the nutrition and seed sources of the river, as they are usually inundated from runoff and groundwater rather than river expansion. The floristic distinction between these two communities seems to be largely a result of time. Field observations of past agricultural activity and differing lengths of time under reduced soil conditions support this conclusion.

The swamp, marsh, and beach communities appear more eccentric to the field observer, an observation supported by their lack of similarity with each other and the remaining communities. The swamp is permanently inundated and canopied. The marsh is permanently inundated but without woody taxa. The beach community is regularly flooded, yet its sandy soil makes it drier than many less frequently inundated sites. These conditions are somewhat self-maintaining; without an annual draw-down of the standing water, the marsh community will not proceed to forestation. This same principle is eliminating trees from the central, no draw-down portion of the swamp. The field observer will notice that the ratio of dead to live trees increases as the distance from the nearest margin of the swamp is increased, forming concentric zones of vegetation around the deepest part. However, as long as the water level does not increase to the point of lake formation, certain woody species, such as *Cephalanthus occidentalis*, will continue to dominate the community. Finally, the beach community may be considered unique in the site not only for its hydrology but also for its constant reception of seeds from the entire upriver Ohio River system.

Species of concern. Ten threatened or endangered species, including one state record, is a considerable number for a single tract of this size in West Virginia indicating a lack of similar habitat in the state necessary to support more populations of these species. This may be expected from the elimination

of much of the floodplain by highlift dams. In his investigation of Ohio River embayments, Ely (1992) recorded two species of concern, *Carex projecta* and *Amorpha fruticosa*, found on the GBWMA list. Only *Carex projecta* and *Eleocharis palustris* appear to be on the fringe of their North American ranges. *Spermacoce glabra* and *Wolffia columbiana* are probably more common in the Ohio River Valley than is now recorded. As previously mentioned, it is likely that *W. columbiana* is quite common, being misidentified as *W. punctata*.

The swamp. A review of Liu (1991) added only two (unvouchered) taxa to the flora. The production of a vouchered flora for this *C. occidentalis*-dominated deepwater swamp community should be the topic of future research.

Summary

A combination of multivariate analysis of quantitative vegetation data and floristic analysis of resultant classifications identified seven distinct and consistent vascular plant communities. These communities are arranged along a moisture gradient as determined by average water depth and species composition.

Stages in community succession are suggested by the quantitatively and qualitatively observed intergrading of margins of various stands. With increased elevation and drainage, river flats grade into streamside forests. With a longer history of inundation, new swales grade into old swales, and old swales grade into swamps. With increasing depth and permanence of inundation, swamp overstory dies, and the community tends toward old buttonbush swamp and then open water.

The communities at GBWMA are species rich and highly native. They contain many rare taxa and are relatively undisturbed. Most of the supporting habitat for these communities has been destroyed in this century.

GBWMA shares more than half of its recorded taxa with areas in two other Ohio River Valley studies of riparian systems.

The seven communities as mapped in Appendix B satisfy the vegetation criterion for classification as wetlands under Federal guidelines (Environmental Laboratory 1987). Soil and hydrology criteria, also required for a final determination, were not evaluated. Note that the 1989 Federal Manual for Identifying and Delineating Jurisdictional Wetlands was not considered.

4 Propagation of Selected Woody Plant Species in A Created Wetland[1]

Introduction

Riparian wetland communities comprise a band of varying breadth where terrestrial and aquatic ecosystems meet and commingle. They are thus true ecotones, characterized by some elements of the upland system, some of the aquatic system, and some unique to the wetland itself (Gregory et al. 1991). As with other wetland attributes, the pattern of vegetation development and persistence is strongly influenced by seasonal and longer-term hydrologic fluctuations. In created wetlands, chance may also play a very significant role in determining plant species composition changes over time (Niering 1990), especially where revegetation relies on resident or transported seed banks or on colonization from neighboring wetland areas (van der Valk 1981, Willard et al. 1990, ter Heerdt and Drost 1994).

This element of chance may be particularly influential when the ultimate intent is a forested wetland, since the generally slower colonization and growth rates of woody plants provide greater opportunity for encroachment by unwanted competitors that may slow or even prevent the establishment of preferred species (Clewell and Lea 1990). Thus, in efforts to create or restore bottomland hardwood forest communities, it is common to rely on some form of direct planting of hardwood species to accelerate the development of a forest structure. Propagules used in direct planting vary from seeds to saplings. Because efforts to create bottomland communities have all been initiated fairly recently, and because of the length of time required for woody plant growth, it is not yet clear what constitutes the "best" method for such plantings (Clewell and Lea 1990). Given that successful plant propagation methods are extremely varied and often highly species-specific (Hartmann, Kester, and Davies 1990), it is likely that successful procedures will depend significantly on the interaction between growth characteristics of the species planted and various attributes (e.g., hydrologic regime, soil properties, climatic variation) of the particular site.

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[1] Jeffrey D. May, Ph.D.

Another consideration in planting is the genetic source of propagules. Several references cite the advantages of regional or, preferably, local sources in that they are more likely to represent ecotypes adapted to local conditions (Clewell and Lea 1990, Mitsch and Gosselink 1993). In addition, from the perspective of conserving genetic diversity, utilizing local stock whenever possible avoids subjecting locally adapted gene pools to dilution by genes of nursery stock bred from plants that evolved in other localities.

The purpose of this study was to assess the practicality of establishing five woody species in a created wetland site by direct planting of cuttings gathered from a nearby bottomland forest. The five species consisted of two tree species, black willow (*Salix nigra* Marshall) and green ash (*Fraxinus pennsylvanica* var. *subintegerrima* (Vahl) Fernald), and three shrub species, common alder (*Alnus serrulata* (Aiton) Willd.), buttonbush (*Cephalanthus occidentalis* L.), and silky dogwood (*Cornus amomum* Miller). Initial expectations, based on Thunhorst (1993), were that cuttings of *S. nigra* and *C. occidentalis* would root easily. Information concerning the other three species was ambiguous or not available.

Methods

This study was carried out at the Corps of Engineers mitigation wetland site at GBWMA, which occupies a portion of the floodplain on the south bank of the Ohio River in Green Bottom, WV (35°00'N, 82°14'W). Development of the wetland was initiated with the completion of a dike by the Corps of Engineers in September 1992, followed by natural filling of the new impoundment area.

Cuttings of the five native wetland species were gathered in early March 1994, from source plants growing within GBWMA 2 km east of the planting site. Cuttings were moistened, placed in plastic bags, and stored at 4 °C until planting in April.

Four plantings were carried out on 1, 8, 9, and 16 April. For each of the five species, each planting consisted of 48 cuttings divided into four "elevation" groups, each group consisting of 12 cuttings planted in two rows of six, 30 cm apart. Individual stems were placed 15 cm apart within rows. In all four plantings, one elevation group was centered on the water line at the time of planting. (Since the water line receded during the planting period, the actual elevation of that group varied.) In the first two plantings, the other elevation groups were centered at 2.3 m and 4.6 m upland from the water line, and 2.3 m into the water, at a depth of 10 cm. The planting pattern was similar in the third and fourth plantings except that the spacing between groups was increased to 3.3 m. For each cutting, a 35-cm spade was inserted into the soil and moved back and forth to create a narrow opening. Then the cutting was inserted, leaving at least one node (usually 5 to 15 cm) above soil level; the adjacent soil was tamped down around the stem.

The first assessment of survivorship was carried out during 10 to 19 May 1994, approximately one month after the final planting. By that time the cuttings were difficult to see clearly because of the growth of the surrounding vegetation. Therefore, all plants within 10 to 15 cm of the cuttings were broken off by hand near soil level prior to the assessment of each group. Cuttings were scored as "alive" if green growth was evident; otherwise, they were considered "dead." A second survivorship assessment was performed on 30 May using the same criteria.

Results

The planted cuttings of all five species averaged 34 cm in length (Table 28) and 7.5 mm in diameter (Table 29); although, *C. amomum* cuttings were generally thinner (mean diameter 4.0 mm) and *C. occidentalis* somewhat thicker (mean diameter 9.4 mm) than those of the other species.

Table 28
Minimum, Maximum, and Mean Length (cm) of Cuttings Planted at the Mitigation Wetland at GBWMA

Species	*n*	Min.	Max.	Mean
Alnus serrulata	38	25	37	31.7
Cephalanthus occidentalis	56	24	42	33.3
Cornus amomum	60	24	54	36.8
Fraxinus pennsylvanica	59	21	49	36.1
Salix nigra	71	23	37	31.6

Note: Data were taken from a subset of size *n* of the 192 planted cuttings of each species.

Table 29
Minimum, Maximum, and Median Basal Diameter (mm) of Cuttings Planted at the Mitigation Wetland at GBWMA

Species	*n*	Min.	Max.	Median
Alnus serrulata	38	3.8	19.4	7.2
Cephalanthus occidentalis	56	4.4	17.4	9.4
Cornus amomum	60	3.0	6.6	4.0
Fraxinus pennsylvanica	59	4.4	14.7	7.6
Salix nigra	71	3.8	19.4	7.5

Note: Data were taken from a subset of size *n* of the 192 planted cuttings of each species.

Of the 192 cuttings planted for each species, 11 were removed by unknown animals. Of the remaining stems, the proportion scored as alive at the first assessment ranged from 69 percent for *F. pennsylvanica* to 99 percent for *S. nigra*, with both *F. pennsylvanica* and *A. serrulata* demonstrating considerably lower survivorship than the other three species (Table 30). For each elevation, the survivorship value was derived by dividing the number of stems bearing green shoots by the number present (i.e., not removed). Because there were no significant differences in survivorship among plantings, the values from all four plantings were combined within each elevation. In *A. serrulata*, survivorship was significantly reduced at the lowest elevation, but there were no differences among elevations for any of the other species.

Table 30
Proportion of Cuttings Direct-Planted During 1-16 April That Were Growing in Mid-May at the Mitigation Wetland at GBWMA

	Elevation[1]				
Species	1	2	3	4	Mean
Alnus serrulata	0.83	0.83	0.81	0.46	0.73
Cephalanthus occidentalis	1.00	0.94	0.97	0.97	0.97
Cornus amomum	1.00	0.94	0.83	0.97	0.93
Fraxinus pennsylvanica	0.65	0.69	0.67	0.77	0.69
Salix nigra	1.00	0.98	1.00	1.00	0.99

[1] Elevations are designated from highest (1) to lowest (4).

At the second assessment on 30 May, whereas the survivorship of *S. nigra*, *C. occidentalis*, and *C. amomum* remained high, half of the *A. serrulata* cuttings that were growing in mid-May had died (Table 31). Survivorship values for *F. pennsylvanica* increased substantially during the same interval.

Discussion

Potential survivorship

After 1-1/2 to 2 months of growth, these plants can provide only a very preliminary indication of their probability for long-term establishment on the GBWMA mitigation site. Of those that had failed to grow by the time of the first assessment (Table 30), some may have had insufficient stored resources to sustain initial root and/or shoot production (Hartmann, Kester, and Davies 1990). For example, Burgess, Hendrickson, and Roy (1990) found significantly lower survivorship for *Salix alba* cuttings less than 6 mm in diameter or 15.2 cm long. However, within the range of stem sizes used here, there was

Table 31
Proportion of Plants That Were Alive in Mid-May Surviving Until 30 May in the Mitigation Wetland at GBWMA

Species	Elevation[1]				Mean
	1	2	3	4	
Alnus serrulata	0.60	0.51	0.48	0.24	0.48
Cephalanthus occidentalis	1.00	0.98	1.00	1.00	0.99
Cornus amomum	0.98	0.94	0.98	0.87	0.94
Fraxinus pennsylvanica	0.94	0.81	0.97	0.87	0.86
Salix nigra	1.00	1.02[2]	1.00	1.00	1.01

[1] Elevations are designated from highest (1) to lowest (4).
[2] Survivorship was greater than 1.00 here because the one *S. nigra* individual that was counted dead in the first assesment developed a shoot from an underground node by the 30 May assessment.

no clear correlation between survivorship and cutting size. That is, for *A. serrulata* and *F. pennsylvanica*, two species exhibiting lower initial success (Table 30), survivors were not significantly different in size from those that failed to grow.

An unknown number of the stems that failed to grow may have been dead at collection time, since they were leafless and bud condition was not always obvious. Ideally, if distinguishing them were possible, these stems would have been omitted from the survivorship data since, not having been alive at the outset, they cannot properly be said to have died during the study. Another unknown portion of dead stems might have died during cold storage. This latter group would be more legitimately included in the survivorship data, since storage is a necessary step in the method of propagation being evaluated here. But there was no basis for distinguishing such stems from those that were dead at collection time or from those that failed to grow from insufficient stored resources.

The second assessment (Table 31) may provide a better indication of potential survivorship in that survivors were based on those that had already shown some growth and were thus clearly not dead at planting time. A very few individuals that were scored as dead in the first assessment were found to have grown by the second assessment; but these were insufficient in number to affect the following conclusions.

Within the short time frame of this study, only *A. serrulata* had already exhibited clear signs that it may not be easily established using spring-planted cuttings. The death of half of the growing individuals over the approximate 2-week period between assessment dates and the apparent lack of vigor in the survivors at the time of the second assessment point to the likelihood that few,

if any, of these individuals will attain maturity. The commercial propagation of some ornamental *Alnus* spp. is carried out from stratified seeds or by the application of rooting hormones to cuttings (Hartmann, Kester, and Davies 1990). Such methods might also improve the effectiveness of direct planting of *A. serrulata.*

An additional consideration of potential importance for this species may be its relationship with root symbionts. *Alnus* species fix atmospheric nitrogen through their association with the streptomycete *Frankia* (Postgate 1982) which, if limited or absent in the soil, may affect the ability of *A. serrulata* to root successfully. A similar problem may arise if *A. serrulata* requires a mycorrhizal associate for healthy growth. Doerr, Redente, and Reeves (1984) found that the colonization and succession of plants in disturbed sites correlated directly with the presence of the propagules of mycorrhizal fungi in the soil. In addition, Cooke, Butler, and Madole (1993) suggested that in wetlands the soil oxygenation associated with seasonal drawdowns may contribute significantly to their characteristic productivity and diversity by improving mycorrhizal activity. It is possible that this may have contributed to the lower survivorship exhibited by *A. serrulata* in the lowest elevation groups in this study.

The increase in apparent survivorship between the two assessments for *F. pennsylvanica* is likely to have resulted from a relatively high proportion of cuttings being dead at the time of planting (reflected as low initial success, Table 30) but a high success rate for those that were alive when planted (Table 31). The consistency between both assessments for *C. occidentalis*, *C. amomum*, and *S. nigra* suggests that these three species may have a reasonable chance for success. However, a number of cautionary considerations (discussed below) may limit that potential to an unknown extent.

Factors potentially limiting ultimate establishment

As is true for other ecosystems, a variety of elements influence the potential establishment of any plant-colonizing wetlands. Given the importance of hydrology as a determinant of plant success (Thunhorst 1993), any seasonal or stochastic event affecting hydrology may critically influence establishment. According to Thunhorst (1993), of the five species, *A. serrulata* and *C. occidentalis* are obligate wetland species, *C. amomum* and *F. pennsylvanica* are facultative wetland species, and *S. nigra* is somewhat in between, being found much more commonly in wetlands than not. In addition, each has different tolerances for depth, frequency, and duration of flooding. Excessive drying or wetting of the soil would therefore be expected to affect the species differentially. In addition to the more-or-less predictable seasonal fluctuations of soil moisture in riparian wetlands, plants are likely to experience stochastic variation of greater magnitude in unusually wet or dry years. Furthermore, plants may have different requirements and tolerances during establishment than do mature plants. For example, constant high soil moisture may be required to induce root formation and development (Hartmann, Kester, and Davies 1990)

even in those plants that would be tolerant of a certain degree of drying once established.

Competition is another factor of potential importance. Because the GBWMA mitigation project is only 1-1/2 years old, the successional changes initiated by the inundation of the former old-field community are still very much in process. Although many upland plants had retained a foothold in the seasonally flooded planting area, they were clearly in decline there. This may suggest that their competitive influence will also decline over the next several years. If the cuttings survive that period, the old-field plants may prove to have been beneficial in the long run by preventing the colonization of undesirable species long enough to permit the establishment of the preferred species.

Herbivory has occasionally been a significant problem in both upland and wetland revegetation projects (Weller 1990, Austin, Urness, and Durham 1994). In this study, although only one willow plant appeared to have been browsed by a large animal, future significant damage cannot be ruled out. All of the five species planted are utilized by white-tailed deer (*Odocoileus virginianus*) or beaver (*Castor canadensis*) for food or shelter (Thunhorst 1993), both of which are present in GBWMA.

Plant success in wetlands can also be affected by more subtle below-ground factors. In addition to the possible role of mycorrhizal associates, a variety of organisms can affect the rate and extent of nutrient cycling in aquatic systems (Webster and Benfield 1986, Gregory et al. 1991, Kok and Van Der Velde 1994). Such processes have received little attention in created wetlands, so it is difficult to determine how rapidly or successfully they become established in such situations.

Conclusions

Considerable work needs to be done to ascertain which if any of these factors will be influential in modulating the successful establishment of these five species at the GBWMA mitigation site. The case of *A. serrulata* appears to be the greatest challenge. The question of the importance of root symbionts to that species could be partially addressed by planting cuttings in soil transported from the base of established individuals in the adjacent bottomland. For all of the species, experimental plantings of cuttings at other times of the year would provide useful data concerning the flexibility of planting schedules in wetland creation. Finally, long-term monitoring of the different plantings will be necessary to determine whether initial successes in root cuttings will be followed by ultimate success in establishing the species in the created wetland.

5 Changes in Soil Physical and Chemical Characteristics[1]

Introduction

Implicit in the "No Net Loss" Policy for wetlands (National Wetlands Policy Forum 1988, Davis 1989) is a mandate that for any area of native wetland which is destroyed by human activity, an equivalent area of wetland must be created in as nearby a location as possible. The Gallipolis (Ohio) Locks and Dam Replacement Project required the draining of nearly 30 ha of native wetlands along the Ohio River. Therefore, in 1992 the Corps of Engineers constructed a series of dikes in an old field within GBWMA, located 27 km northeast of Huntington, West Virginia, to mitigate the loss of wetland habitat. The construction of this mitigation wetland site offered a unique opportunity to study changes in some of the soil processes that occur during transformation from a terrestrial into a wetland ecosystem.

The most immediate change that occurs in soil following inundation is the rapid depletion of O_2 and the establishment of reducing conditions, a process which may take as little as several hours or as much as several days (Mitsch and Gosselink 1993). Cogger, Kennedy, and Carlson (1992) found a change in soil oxidation-reduction (redox) potential from + 600 mV to 300 mV in <35 d following flooding in experimentally flooded soils in the Puget Lowland of western Washington. Most of the other changes in post-inundation soil are related either directly or indirectly to these low redox conditions.

Nitrate reduction follows shortly after O_2 depletion during inundation. Nitrate present in the soil can become reduced either to NH_4^+ or to N_2O or N_2 (denitrification), the end-point of reduction being largely dependent on amounts of organic matter present (Reddy and Graetz 1988, Mitsch and Gosselink 1993).

[1] Frank S. Gilliam, Ph.D.

Following NO_3^- reduction on the redox potential scale are Mn^{4+} and then Fe^{3+} reduction at 250, 225, and 120 mV, respectively (Mitsch and Gosselink 1993). Both Mn and Fe exist in very stable, insoluble oxidized states, becoming more soluble and available when reduced.

Similar to changes in Mn^{4+} and Fe^{3+} under reducing conditions, phosphorus (P) availability generally increases following flooding. P is either organically-bound or largely present as phosphate (PO_4^{3-}), which is bound in a variety of forms, including ferric and aluminum phosphates. As Fe^{3+} is reduced to Fe^{++} under low redox conditions, PO_4^{3-} bound as $FePO_4$ can be released (Hossner and Baker 1988). Thus, for soils high in Fe, post-inundation P dynamics should follow closely those of Fe. Changes in availability of macronutrient cations (e.g., Ca^{++}, Mg^{++}, and K^+) and other micronutrient metals (e.g., Zn^{++} and Cu^{++}) in flooded soils have been less well studied (Gilmour and Gale 1988).

Objectives of Study

The purpose of this study was to examine changes in several soil physical and chemical components during the creation of a mitigation wetland at GBWMA. More specifically, these components included soil redox potential, soil texture, organic matter, and extractable macronutrients (N, P, K, Ca, and Mg) and micronutrients (Fe, Mn, Zn, and Cu).

Methods and Materials

Field sampling and analysis

A total of 10 sample plots was located in three different areas within GBWMA. Six (two transects of three plots each) were located in the old-field. These parallel transects were established to span an elevation gradient from approximately 168 m to 165 m above mean sea level. Plot 1 (~168 m) was high enough in elevation to avoid inundation during the wetland creation process. Therefore, data from these plots (i.e., Plot 1 from both transects) will be referred to as "old-field" for both the pre- and post-inundation periods. Plots 2 and 3 were established low enough in elevation to experience inundation. Thus, they will be referred to as "old-field" for the pre-inundation period but will be referred to as "mitigation wetland" for the post-inundation period. The four remaining sample plots were located in adjacent Green Bottom Swamp, two in each of two swamp types: a "young" swamp, approximately 4-years old following dam construction by beaver activity; and an "old" swamp, Green Bottom Swamp proper.

Pre-inundation sampling took place 9 September 1992, concurrent with the construction and near completion of dikes by Corps of Engineers personnel. Post-inundation sampling took place 16 September 1993. During this period,

water had time to accumulate passively in the designated areas, being blocked from natural flow by the dikes. Standing water had been present for approximately 8 months by the time of post-inundation sampling.

Redox was measured in situ by inserting an Orion platinum redox electrode (Model 96-78) directly into the soil at depths of 10 and 20 cm. The electrode was attached to an Orion portable pH/ISE meter (Model 250 A). Because of great spatial variability in redox conditions, three measurements were taken at each depth plot. These three values were averaged for one mean redox value per plot at each soil depth.

Soils were sampled at depths of -10 cm and 10 to 20 cm. Three cores were taken with a 2-cm diam soil probe at each plot. Each core was then divided into the two depths, after which all three cores were combined to yield a single composite soil sample per depth at each plot. All soils were returned to the laboratory at MU where they were dried, ground, and sieved to pass a 2-mm screen. Although this type of preparation has been shown to alter extractability of ions (Gilliam and Richter 1985, 1988), drying, grinding, and sieving in this case offered greater quality control of data, since samples had to be shipped for analysis (explained below). It should be noted that, as a result of a lack of structure, a distinct separation between these depths was not possible for the young swamp plots. Therefore, these data will be expressed as a single 0 to 10 cm depth.

Soil texture was determined on all composite samples using the hydrometer method (Bouyoucos 1951; Gilliam, Yurish, and Goodwin 1993). Sub-samples of soil were sent to the University of Maine Soil Testing Service and Analytical Laboratory for analysis. Organic matter was measured with the loss-on-ignition method (Gilliam and Turrill 1993). Water-extractable pH was measured with a glass electrode. Extractable P, Ca, Mg, K, Fe, Mn, Cu, and Zn were determined with plasma emission following extraction with ammonium acetate (pH 4.8). NO_3^-N and NH_4-N were measured with autocolorimetry following 1:10 (w:v) extraction with 1 N KC1. Cation exchange capacity (CEC) was calculated by summing exchangeable acidity and extractable Ca, Mg, and K.

Data analysis

Pre-inundation period means of all measured variables were compared among three site types (old-field, young swamp, and old swamp) using analysis of variance and Duncan's multiple range testing (Proc ANOVA, SAS 1982), separated by soil depth. Pre-inundation data were also subjected to Pearson product-moment correlation (Proc CORR, SAS 1982; Zar 1984). For this correlation, data from both young and old swamp plots were combined for a single "swamp" correlation matrix.

Data were regrouped into three different site types for post-inundation data analysis. As mentioned earlier, the two highest elevation old-field plots

retained their old-field designation. However, the four lower elevation old-field plots were changed to "mitigation swamp," since they had been flooded for the 8-month period. The two swamp sites once again were combined into "swamp." Pre- versus post-inundation means for all variables, separated by site and depth, were compared using t-tests (Proc TTEST, SAS 1982). Finally, post-inundation period data were subjected to correlation analysis for mitigation swamp and swamp sites separately.

Results

Soils were significantly different ($p < 0.05$) among site types for redox potential, texture (sand and clay content only), CEC, and organic matter, with old-field soil having higher redox, sand content, CEC, and organic matter and lower clay content relative to the two swamp sites (Table 32). The two swamp sites were not significantly different from each other for any of the measured variables shown in Table 32, nor were they significantly different from each other in pH or extractable macro- or micronutrients (Table 33). Old-field soils were significantly different ($p < 0.05$) from both swamp sites for pH and most extractable nutrients (Table 33). In general, pH, NO_3, Ca, Mg, and Zn were higher in old-field soils than in swamp soils. In contrast, NH_4, P, Fe, and Mn were lower in old-field soils. K and Cu were not significantly different among sites (Table 33).

Correlation analysis revealed numerous significant correlations ($p < 0.05$) among soil variables of the old-field for pre-inundation sampling. Most notable were the many significant correlations of organic matter with other soil variables (12 out of a possible total of 17) (Table 34). The same analysis revealed far fewer significant correlations ($p < 0.10$) among soil variables of the swamp plots for the pre-inundation period (Table 35). It should be noted that a different level of acceptability was established for significant correlations for the swamp data compared with those for the old field because of the lower sample size from the swamp plots for this analysis.

Redox potential declined significantly ($p < 0.01$) from the pre- to the post-inundation period for all site types and all depths, except for the 0- to 10-cm depth of the swamp site, which showed a significant decline at ($p < 0.10$) (Table 36). Significant changes in texture (particle size) classes and CEC were mostly found for the mitigation wetland site. Organic matter declined significantly ($p < 0.10$) for all sites and depths but was more pronounced and significant ($p < 0.01$) for the mitigation wetland site.

Except for the NH_4 at 10 to 20 cm, there were no significant changes in macronutrients through time for the old-field site (Table 37). Mitigation-wetland soils decreased significantly ($p < 0.10$) in NO_3, P, an Ca at the 0- to 10-cm depth; NH_4 increased significantly ($p < 0.05$) at both depths in these soils. Swamp soils showed significant changes for NO_3, P, and Mg (Table 37).

Table 32
Mean Values for Several Soil Variables in Old Field, Young Swamp, and Old Swamp at GBWMA

Site	Depth, cm	Redox, mV	Sand, %	Clay, %	Silt, %	CEC, meq/100g	OM, %
Old Field	0-10	$+273.9^{a}$	26.2^{a}	19.6^{b}	54.2^{a}	10.5^{a}	8.9^{a}
	10-20	$+282.6^{a}$	18.4^{a}	25.2^{b}	56.4^{a}	10.0^{a}	7.6^{a}
Young Swamp	0-10	-298.5^{b}	8.5^{a}	36.3^{a}	55.2^{a}	7.5^{b}	6.0^{a}
	10-20	---	---	---	---	---	---
Old Swamp	0-10	-156.2^{b}	8.8^{a}	35.3^{a}	56.0^{a}	6.0^{b}	5.8^{b}
	10-20	-176.8^{b}	5.8^{a}	37.2^{a}	57.1^{a}	6.2^{b}	5.0^{b}

Note: Means followed by the same superscript are not significantly different among sites for a given sample depth at $p < 0.05$.

Table 33
Mean Values for pH and Extractable Macro- and Micronutrients from Old Field, Young Swamp, and Old Swamp Soils at GBWMA

Site	Depth cm	pH	NO_3 mg/kg	NH_4 mg/kg	P mg/kg	Ca mg/kg	K mg/kg	Mg mg/kg	Fe mg/kg	Mn mg/kg	Cu mg/kg	Zn mg/kg
Old Field	0-10	5.67^{a}	6.8^{a}	4.8^{c}	3.6^{b}	1565^{a}	127^{a}	258^{a}	29^{b}	36^{b}	2.2^{a}	11.7^{a}
	10-20	5.80^{a}	4.5^{a}	3.4^{b}	2.5^{b}	1539^{a}	83^{a}	244^{a}	17^{b}	23^{b}	2.4^{a}	9.3^{a}
Young Swamp	0-10	5.15^{b}	0.5^{b}	74.3^{a}	6.0^{a}	964^{b}	150^{a}	145^{b}	239^{a}	148^{a}	2.7^{a}	4.8^{b}
	10-20	---	---	---	---	---	---	---	---	---	---	---
Old Swamp	0-10	5.20^{ab}	0.8^{b}	60.8^{a}	6.4^{a}	769^{b}	188^{a}	112^{b}	273^{a}	165^{a}	2.4^{a}	5.5^{b}
	10-20	5.40^{a}	0.7^{b}	45.3^{a}	4.7^{a}	874^{b}	97^{a}	132^{b}	207^{a}	220^{a}	2.9^{a}	2.9^{b}

Note: Means followed by the same superscript are not significantly different among sites for a given sample depth at $p < 0.05$.

Table 34
Correlations of Pre-inundation Period Soil Variables Among Old-Field Plots of GBWMA

	Redox	Sand	Clay	Silt	pH	Ca	K	Mg	P	Cu	Fe	Mn	Zn	NO_3	NH_4	CEC
Sand	-0.74															
Clay	0.57	-0.93														
Silt	0.81	-0.83	---													
pH	---	---	---													
Ca	-0.59	---	---	-0.87	0.79											
K	---	---	---	---	---	---										
Mg	---	---	---	---	0.79	0.86	---									
P	---	0.72	-0.63	-0.66	---	---	---	---								
Cu	-0.64	---	---	---	---	---	---	---	---							
Fe	-0.61	0.75	-0.78	---	---	---	---	---	0.72	0.63						
Mn	-0.59	0.86	-0.79	-0.74	---	---	---	---	0.94	---	0.81					
Zn	---	0.82	-0.85	---	---	---	---	---	0.74	---	0.70	0.78				
NO_3	---	---	---	---	---	---	---	0.70	---	---	---	---	---			
NH_4	---	---	---	---	---	---	---	---	---	---	---	---	---	---		
CEC	-0.58	---	---	-0.86	0.68	0.96	---	0.90	0.68	---	---	0.66	---	0.69	---	
OM	-0.58	0.83	-0.70	-0.78	---	0.71	---	0.58	0.90	---	0.64	0.93	0.78	---	---	0.80

Note: Values shown are Pearson product-moment correlation coefficients (r) significant at $p < 0.05$.

Table 35
Correlations of Pre-inundation Period Soil Variables Among Swamp Plots at GBWMA

	Redox	Sand	Clay	Silt	pH	Ca	K	Mg	P	Cu	Fe	Mn	Zn	NO_3	NH_4	CEC
Sand	---															
Clay	---	---														
Silt	---	-0.86	---													
pH	---	---	---	---												
Ca	-0.79	---	---	---	---											
K	-0.79	---	---	---	---	---										
Mg	-0.83	---	---	---	---	0.94	---									
P	---	---	---	---	---	---	---	---								
Cu	---	---	---	---	---	---	---	---	---							
Fe	---	---	---	---	---	---	---	---	0.95	---						
Mn	---	---	---	---	0.97	---	---	---	---	-0.75	---					
Zn	---	---	---	---	-0.88	---	---	---	0.78	---	---	---	-0.90			
NO_3	---	---	---	---	---	---	---	---	---	---	---	---	---			
NH_4	---	---	---	---	---	---	0.95	---	---	---	---	---	---	---		
CEC	-0.93	---	---	---	---	0.83	0.77	0.77	---	---	---	---	---	---	---	
OM	---	---	---	-0.77	---	---	---	---	0.87	---	0.77	---	0.85	---	---	---

Note: Data include samples from both young and old swamp combined. Values shown are Pearson product-moment correlation coefficients (r) significant at $p < 0.10$.

Table 36

T-Test Comparisons of Pre- versus Post-inundation Period Means of Several Soil Variables in Old-Field (OF), Mitigation-Wetland (MW), and Swamp (SW) Sites

Site	Depth, cm	Redox, mV		Sand, %		Clay, %		Silt, %		CEC, meq/100g		OM, %	
		Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post
OF	0-10	400.1[1]	-16.9	14.9	16.6	26.7	24.4	58.5	59.1	9.4	10.1	7.5[2]	10.8
	10-20	428.6[1]	6.3	8.3	14.3	28.7	31.4	63.1[3]	54.3	8.7	8.9	6.8	9.4
MW	0-10	210.9[1]	-280.5	31.9[2]	22.3	16.4[2]	24.7	52.1	53.0	11.1	9.4	9.6[1]	13.0
	10-20	209.6[1]	-294.6	23.4	20.7	23.5	27.1	53.0	52.2	10.6	10.4	8.0[1]	12.2
SW	0-10	-227.3[2]	-326.6	8.6	7.7	35.8[3]	39.0	55.6	53.4	6.7	6.6	5.9[1]	9.6
	10-20	-176.8[1]	-335.7	5.8	7.1	37.2	38.3	57.1	54.6	6.2	6.8	5.0[1]	8.9

[1] Indicates significant difference between pre- and post-inundation period means at $p < 0.01$.
[2] Indicates significant difference between pre- and post-inundation period means at $p < 0.10$.
[3] Indicates significant difference between pre- and post-inundation period means at $p < 0.05$.

Table 37

T-Test Comparisons of Pre- versus Post-inundation Period Means of Extractable Macronutrients in Soils From Old-Field (OF), Mitigation-Wetland (MW), and Swamp (SW) Sites

Site	Depth, cm	NO_3		NH_4		P		Ca		K		Mg	
		Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post
OF	0-10	6.7	0.8	5.2	2.5	3.0	3.7	1,346	1,410	142	145	242	263
	10-20	1.9	1.0	3.4[1]	1.8	2.1	2.3	1,315	1,323	76	94	213	218
MW	0-10	6.8[2]	1.8	4.6[2]	62.7	3.9[1]	3.0	1,675[1]	1,406	120	118	266	226
	10-20	5.9	5.8	3.4[2]	20.8	2.8	2.6	1,651	1,614	86	88	260	265
SW	0-10	0.7[2]	0.1	67.5	62.5	6.2[2]	3.8	866	816	134	120	121	121
	10-20	0.7	0.5	45.3	37.0	4.7[1]	2.9	874	915	97	99	132[2]	148

Note: Unit for all values is mg micronutrients/kg soil.
[1] Indicates significant difference between pre- and post-inundation period means at $p < 0.10$.
[2] Indicates significant difference between pre- and post-inundation period means at $p < 0.05$.

Except for Cu at both sample depths, there were no significant changes in micronutrients through time for old-field soils (Table 38). Cu decreased significantly through time in both mitigation-wetland and swamp soils, although this was more significant ($p < 0.01$ and $p < 0.01$ for 0- to 10- and 10- to 20-cm depths, respectively) in the mitigation wetland than the swamp. There were pronounced changes through time in Fe for both wetland types, but in the mitigation wetland this was a significant increase ($p < 0.10$), while in the swamp it was a decrease ($p < 0.05$) (Table 38).

Correlation analysis produced several significant correlations ($p < 0.01$) among measured variables in the mitigation wetland soils, five of which were with organic matter (Table 39). In contrast, correlation analysis for swamp soil data resulted in far fewer significant correlations, none of which were with organic matter (Table 40).

Discussion

Results of this study will be examined in two ways. First, pre-inundation period comparisons will be made and discussed among site types, especially between the old-field and the two swamp soils as a whole. Second, patterns of similarities and differences between these two site types will be used to generate predictions concerning change in the inundated soils over time. In other words, it will be predicted that, for a given variable, change (or lack of change) through time in the mitigation wetland plots will resemble the pattern of difference or similarity for that variable between old-field and swamp soils as seen in Tables 32 and 33.

Pre-inundation comparisons between old-field and swamp soils

Pre-inundation differences between old-field and swamp soils were consistent with what would be predicted for changes in soil processes under flooded conditions. Mitsch and Gosselink (1993) described a pattern of such change over time as a sequence of reduction reactions involving a variety of soil constituents in the following order: 1) O_2 reduction, 2) NO_3^- reduction (NH_4^+, N_2O, or N_2), 3) gradual increases in NH_4 and PO_4, 4) reduction of relatively insoluble Mn^{4+} (resulting in increases in more soluble Mn^{2+}), and 5) Fe^{3+} reduction (increases in Fe^{2+}). Gilmour and Gale (1988) found either slight decreases or no appreciable change for Cu^{2+} and Zn^{2+} in flooded soils. Ca^{2+}, Mg^{2+}, and K^+ exhibited patterns similar to those for Cu^{2+} and Zn^{2+}. Less is known about the effects of flooding on soil texture.

Old-field soils at GBWMA were under oxidizing conditions with a redox potential of +400 mV and were of a silt loam texture. Swamp soils, decidedly reducing at about -200 mV, were of a silty clay loam texture. CEC of old-field soils was moderate, being greater than the 4.1- to 5.1-meq/100-g range reported by Gilliam and Turrill (1993) for some West Virginia forest sites.

Table 38
T-Test Comparisons of Pre- versus Post-inundation Period Means of pH and Extractable Micronutrients in Soils From Old-Field (OF), Mitigation-Wetland (MW), and Swamp (SW) Sites

Site	Depth	pH		Fe		Mn		Cu		Zn	
		Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post
OF	0-10	5.50	5.60	12	13	23	21	1.6[1]	0.9	10.7	10.7
	10-20	5.60	5.65	13	13	16	13	2.0[2]	1.1	8.3	8.8
MW	0-10	5.75	5.68	37.[2]	112	42	46	2.5[1]	1.6	12.2	10.3
	10-20	5.90	5.95	20.[2]	36	26	36	2.7[3]	1.5	9.7	8.5
SW	0-10	5.18	5.10	256.[1]	176	156	189	2.6[2]	1.8	5.1	6.2
	10-20	5.40	5.33	207.[1]	109	220	175	2.9	1.5	2.9	3.9

Note: Unit for all micronutrients is mg/kg soil.
[1] Indicates significant difference between pre- and post-inundation period means at $p < 0.05$.
[2] Indicates significant difference between pre- and post-inundation period means at $p < 0.10$.
[3] Indicates significant difference between pre- and post-inundation period means at $p < 0.01$.

Table 39
Correlations of Post-inundation Period Soil Variables Among Mitigation-Wetland Plots at GBWMA

	Redox	Sand	Clay	Silt	pH	Ca	K	Mg	P	Cu	Fe	Mn	Zn	NO_3	NH_4	CEC
Sand	0.72															
Clay	---	-0.75														
Silt	---	---	---													
pH	---	---	---	---												
Ca	---	---	---	---	0.95											
K	0.79	0.76	---	---	-0.83	-0.77										
Mg	---	---	---	---	0.98	0.96	-0.82									
P	---	---	---	---	---	---	---	---								
Cu	---	---	---	---	---	---	---	---	0.97							
Fe	---	---	---	---	-0.95	-0.87	0.74	-0.96	0.76	0.70						
Mn	---	---	---	---	---	---	---	---	0.97	---	---					
Zn	---	---	---	---	-0.83	-0.73	---	-0.87	0.90	0.86	0.94	0.82				
NO_3	---	---	---	---	0.77	0.74	---	0.77	---	---	-0.83	---	---			
NH_4	0.72	0.74	---	---	-0.89	-0.88	0.98	-0.89	---	---	---	---	---	-0.70		
CEC	---	---	---	---	0.93	0.99	-0.77	0.94	---	---	-0.84	---	---	0.75	-0.88	
OM	0.74	---	---	---	---	-0.81	0.71	---	---	---	---	---	---	---	0.79	-0.84

Note: Values shown are Pearson product-moment correlation coefficients (r) significant at $p < 0.05$.

Table 40
Correlations of Post-inundation Period Soil Variables Among Swamp Plots at GBWMA

	Redox	Sand	Clay	Silt	pH	Ca	K	Mg	P	Cu	Fe	Mn	Zn	NO_3	NH_4	CEC
Sand	---															
Clay	---	---														
Silt	---	---	---													
pH	---	---	---	---												
Ca	---	---	---	---	0.93											
K	---	---	---	---	---	---										
Mg	---	---	---	---	0.92	0.96	---									
P	---	---	---	---	---	---	---	---								
Cu	---	---	---	---	-0.88	-0.77	---	---	---							
Fe	---	0.79	---	---	---	-0.78	---	-0.80	0.95	---						
Mn	---	---	---	---	---	---	---	---	---	---	---					
Zn	---	---	---	---	-0.79	-0.92	---	-0.90	---	---	0.70	-0.73				
NO_3	---	---	---	---	---	---	---	---	---	---	---	---	---			
NH_4	---	---	---	---	---	---	---	-0.71	---	---	---	---	---	-0.79		
CEC	---	---	---	---	---	0.83	---	0.78	---	---	---	---	-0.87	---	---	
OM	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---

Note: Data include samples from both young and old swamp combined. Values shown are Pearson product-moment correlation coefficients (r) significant at $p < 0.05$.

Organic matter was somewhat low for the old-field soils, less than the 13.8 to 14.2-percent range reported for the same West Virginia forests (Gilliam and Turrill 1993). Both CEC and organic matter were significantly lower in swamp soils compared to old-field soils (Table 32).

Data confirm that many ionic constituents of terrestrial soils are quite sensitive to redox conditions. Because protons (H^+) dominate the soil system under reducing conditions, pH is ~0.5, a pH unit lower in swamp soils than in old-field soils (Table 33). Cations such as Ca^{2+}, Mg^{2+}, and Zn^{2+} become less soluble under reducing conditions and are thus lower in swamp soils, whereas relatively insoluble Mn^{4+} and Fe^{3+} are reduced to more soluble Mn^{2+} and Fe^{2+}, respectively, under these conditions and are higher in swamp soils compared to old-field soils (Table 33).

The response of extractable N is somewhat more complex. The available (extractable) forms of N are fairly equally balanced between NO_3^- and NH_4^+ in the old-field soils. The anaerobic conditions of the swamp soils, however, prevent nitrification. Consequently, there is little N in the form of NO_3^-; >98 percent of extractable N is in the form of NH_4^+. It should be noted that the N data in Table 33 represent pools of available N, not fluxes (total availability) of N. Therefore, what appears to be higher available N for swamp soils (46 to 75 mg N/kg soil versus ~10 mg N/kg soil for old-field soils) is most likely a result of lower uptake of N by swamp vegetation, resulting in an accumulation (greater pool) of N as NH_4^+ in swamp soils.

Correlation matrices for pre-inundation period data from both site types strongly suggest the importance of organic matter in determining nutrient availability and fertility of old-field soils. There were numerous significant correlations among most variables, and all but three nutrients were significantly correlated with organic matter for these soils. Furthermore, organic matter was important in determining the cation exchange capacity in old-field soils, being significantly correlated ($r = 0.80$, $p < 0.05$) with CEC (Table 34). Organic matter also appeared to respond to soil texture, being correlated negatively with clay and silt, and positively with sand content. Fewer significant correlations in the swamp soils (Table 35) suggest that significantly lower organic matter in these soils (Table 32) results in much less influence of organic matter on nutrient availability and that there may be a shift form organic matter to mineral sediments as a predominant factor determining the availability of nutrients in true wetland soils.

Pre- versus post-inundation comparisons

For the pre- versus post-inundation period comparisons, the two highest elevation old-field plots serve as an "old-field control" and the four swamp plots (two each in young and old swamps) serve as "swamp control," since none of these plots experienced any experimental manipulation during the 1-year study period. The four lower-elevation old-field plots (hereafter referred to as "mitigation wetland") are therefore the treatment plots in this

design, having received the experimental treatment of inundation for 8 months prior to resampling.

Predictably, there were few significant changes during the 1-year period in soil physical and chemical characteristics in either control site types. Changes found were likely related to normal seasonal fluctuations in ambient conditions for the old-field swamp sites. The most pronounced differences were for redox potential and organic matter (Table 32). Redox potential decreased substantially in soils of both sites, from just over +400 mV to ~0 mV for the old field. This underlines the sensitivity of redox measurements to antecedent conditions and events; it had rained just prior to these measurements. Declines for the swamp are more difficult to interpret. Indeed, all redox data presented here should be interpreted with caution, since there is no accepted method for in situ measurement of redox potential (Cogger, Kennedy, and Carlson 1992). Increases in organic matter at both sites may be related to seasonal differences in plant productivity and detritus formation.

Based on site comparisons in Tables 32 and 33, pre- versus post-inundation comparisons of the mitigation-wetland plots were mixed with respect to what was predicted. Several changes through time for these plots were consistent with what was predicted. Redox potential decreased from ~+210 mV to ~290 mV, indicating a distinct shift from oxidizing to reducing conditions in the soil. Sand content decreased, while clay content increased, suggesting that sand-sized particles which are stable under oxidizing conditions become unstable under reducing conditions.

Changes in extractable N were also consistent with predictions, with significant decreases in NO_3^- coupled with increases in NH_4^+ (Table 37). Although some of this pattern may be explained as reduction of NO_3^- to NH_4^+ (Mitsch and Gosselink 1993), most is likely the result of two changes brought about by flooding: 1) inhibition, under anaerobic conditions, of nitrification of NH_4^+ to NO_3^-, which is otherwise pronounced in old-field soils;[1] and 2) decreased uptake of available N from extensive mortality of old-field plant species under water-logged soil conditions. The result is a decrease in the soil NO_3^- pool and a large accumulation of NH_4^+.

Other changes in mitigation-wetland soils consistent with predictions involved Ca and Fe. Ca decreased significantly through time (Table 37), whereas Fe increased significantly through time in these soils (Table 38). Similar to depth-related differences in N response to flooding, these changes were much more substantial in the 0- to 10-cm depth than in the 10- to 20-cm depth.

Several other measured variables exhibited responses to inundation which were not consistent with what was expected from the site comparisons in Tables 32 and 33. For example, such comparisons predicted changes through

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[1] Unpublished Data, F. S. Gilliam, 1994, Marshall University, Huntington, WV.

time for pH, Mn, Mg, and Zn, none of which was significantly different between pre- and post-inundation mitigation-wetland soils (Tables 37 and 38). These comparisons also predicted that organic matter would decrease in mitigation-wetland soils over time. To the contrary, organic matter increased significantly (Table 36). Much of this increase may have been related to increased detritus formation from extensive mortality of old-field plants. This detritus would have been both aboveground in the form of stems and leaves and, more important, below ground in the form of rhizomes, roots, and fine roots.

Although extractable P was predicted to increase under inundated conditions, P decreased significantly (Table 37). A proposed mechanism for increases in extractable P is that P is released upon the reductive dissolution of phosphate minerals associated with Fe and Mn (Hossner and Baker 1988). Apparently this has not occurred in mitigation-wetland soils. Observed decreases in extractable P might also be an artifact of the effect of soil drying and grinding, which can substantially influence P extractability (Daughtrey, Gilliam, and Kamprath 1973; Anderson and Beverly 1985; Gilliam and Richter 1985, 1988).

Significant correlations among variables were almost as numerous for mitigation swamp soils as they were for pre-inundation old-field soils (Tables 34 and 39). As with the old-field soil data, organic matter was correlated with several nutrients (although fewer in Table 39 compared with Table 34). In contrast, few significant correlations existed among variables for the same time period (post-inundation) in swamp soils; no correlations existed with organic matter (Table 40).

Conclusions

Results of this study indicate that mitigation wetland soils are developing toward true wetland (hydromorphic, *sensu* Buol and Rebertus 1988) soils following 8 months of inundation. Conditions in these soils are distinctly reducing, causing a significant change in the dynamics of several nutrients, especially N and Fe, which are typical of hydromorphic soils (Mitsch and Gosselink 1993). However, the mitigation-wetland soils also lack some of the characteristics of hydromorphic soils, certainly those of the swamp soils of GBWMA. Most notably are lower extractable Mn and P and higher organic matter. Therefore, it is concluded that 8 months is an insufficient period of time for a complete change in these soils.

As a final note, the striking similarities between the young swamp and the old swamp (Green Bottom Swamp) in this study are quite meaningful. The area of the young swamp, adjacent to Green Bottom Swamp, was much like the old-field site used in this study before the construction of a beaver dam ~4 years ago. This suggests that 4 years may be a sufficient period of time for terrestrial soils of this area to be converted to hydromorphic soils during the process of wetlands creation.

6 Nitrogen Transformations[1]

Introduction

The construction of a mitigation wetland at GBWMA offered a unique opportunity to study changes in some of the soil processes that occur during transformation from a terrestrial into a wetland ecosystem. A previous study at this site (Gilliam 1993) concluded that while the inundated soils of the mitigation site were indeed changing toward true hydromorphic soils (Buol and Rebertus 1988), the 8-month period of the study was an insufficient period of time for a complete change. Further changes in physical and chemical characteristics were anticipated (Gilliam 1993).

Following the rapid depletion of O_2 and the establishment of reducing conditions (a process which may take from as little as several hours to as much as several days) (Mitsch and Gosselink 1993), the most immediate changes following inundation occur in the nitrogen (N) dynamics of the soil. For example, nitrate reduction follows shortly after O_2 depletion during inundation. Soil nitrate, present largely in the soil solution, can become reduced either to NH_4 or to N_2O or to N_2 (denitrification), the end-point of reduction being largely dependent on amounts of organic matter (Reddy and Graetz 1988, Mitsch and Gosselink 1993). Further nitrification of NH_4 is essentially eliminated under these reducing conditions, which, in the absence of plant uptake, may result in the accumulation of NH_4.

The purpose of this study was to examine changes in several aspects of soil N dynamics following the creation of a mitigation wetland at GBWMA. More specifically, testing addressed the following conclusions of the previous study at this mitigation-wetland site concerning changes in soil N following inundation (Gilliam 1993): 1) available (extractable) N exhibits a substantial shift following inundation of old-field soils from relatively equal amounts of NO_3 and NH_4 to a near-total predominance of NH_4; 2) extractable N is significantly greater following inundation of old-field soils because of accumulation of NH_4, the result of anaerobic inhibition of nitrification and decreased uptake of N from extensive mortality of terrestrial vegetation under water-logged conditions.

[1] Frank S. Gilliam, Ph.D.; Mark A. Fisher.

Methods and Materials

Soils of GBWMA are predominantly alluvial in origin and are deep, typically level, and well to poorly drained. Old-field soils used in this study are fine-silty, mixed, mesic fluvaquentic eutrochrepts of the Lindside series (Cole 1989). Soil textures range from clay loams to silty clay loams (Table 41).

Table 41
Texture (Sand, Silt, and Clay), Organic Matter (O.M.), and pH (H_2O- and KCl-extractable) For Soils From Old-Field (OF), Transition (TR), and Mitigation-Wetland (MW) Sites

Site	Sand, %	Silt, %	Clay, %	O.M., %	pH(H_2O)	pH(KC1)
OF	26.0 ± 1.3[a]	44.5 ± 1.0[b]	29.6 ± 1.3[b]	10.0 ± 0.0[a]	6.11 ± 0.05[b]	4.67 ± 0.07[b]
TR	25.8 ± 2.2[a]	45.0 ± 1.8[b]	29.7 ± 1.8[b]	9.9 ± 0.1[a]	6.33 ± 0.07[a]	4.98 ± 0.06[a]
MW	8.0 ± 2.5[b]	52.3 ± 1.4[a]	39.7 ± 1.2[a]	10.4 ± 0.2[a]	6.40 ± 0.06[a]	4.75 ± 0.02[b]

Note: Values shown are means of five transects ± one standard error of the mean. Means followed by the same superscript are not significantly different between sites at $p < 0.05$.

Field sampling and analysis

Soil was sampled from plots established along five parallel transects spanning three distinct habitat types, based on the degree of inundation during wetland construction: 1) old-field (OF, permanently exposed), 2) transition (TR, beneath 10 to 20 cm water and experiencing seasonal exposure and inundation from fluctuations in the water table), and 3) mitigation wetland (MW, permanently inundated beneath ≤1.5 m water). One plot was located within each habitat type along each transect for a total of 15 plots for the study. Transects were 15 m apart oriented in an east-west direction within a given habitat type.

Soils were sampled at depths of 0 to 5 cm. Samples were taken with either a hand shovel (OF plots) or a special sediment corer (TR and MW plots). Mineral soil from each plot was divided into two subsamples, and each subsample was placed in a polyethylene bag. One was incubated in situ by burying it 5 cm beneath the soil surface (the "buried bag" technique, Eno 1960) for ~28 days, while the other was brought back to the laboratory at MU for extraction and analysis. Data presented in this report represent sampling on 18 April and 23 May 1994.

Subsamples of soil from paired sample bags (one incubated and one brought back to the laboratory immediately after sampling) were extracted for N analysis to determine net mineralization and nitrification. Subsamples were extracted with 1N KC1 (10:1 v:w) and analyzed for NH_4 with an Orion 720A pH/ISE meter and NH_4 electrode. Separate subsamples were extracted with

deionized H_2O (10:1 v:w) and analyzed for NO_3 with an Orion 720A pH/ISE meter and NO_3 and reference electrodes. A glass pH electrode was also used to determine pH of extracts. Net mineralization was calculated as incubated (buried) soil NH_4 plus NO_3 minus initial soil NH_4 plus NO_3. Net nitrification was calculated as incubated soil NO_3 minus initial soil NO_3.

Other subsamples of soil returned to the laboratory were dried, ground, and sieved to pass a 2-mm screen. These soils subsamples were analyzed for texture using the hydrometer method (Bouyoucos 1951; Gilliam, Yurish, and Goodwin 1993). Organic matter was measured with the loss-on-ignition method (Gilliam and Turrill 1993).

Data analysis

Means of all measured variables were compared among the three site types (OF, TR, and MW) using ANOVA and Duncan's multiple range testing (SAS 1982). April versus May comparisons of extractable NO_3 and NH_4 were made for each site type via T-tests (Zar 1984). Unless otherwise stated, significant differences were determined at the $p < 0.05$ level.

Results

Soil texture varied somewhat among the three site types, with MW being significantly lower in sand and higher in silt and clay compared with OF and TR (Table 41). In contrast, there were no significant differences among sites with respect to organic matter, with an overall mean for all sites combined of 10.1 percent organic matter (Table 41). There were small but significant differences among sites for both H_2O- and KC1-extractable pH and large discrepancies between the types of soil pH measurement, regardless of site type (Table 41).

Although the inundated sites (TR and MW) were significantly higher in extractable NO_3 in pre-incubation soils than OF, only OF exhibited a significant increase in NO_3 during the incubation period (net nitrification) (Table 42). Extractable NH_4 exhibited a distinct gradient from MW>TR>OF in both pre- and post-incubation samples (Table 42).

ANOVA and Duncan's multiple range test reveal no significant differences among the sites for daily rates of net nitrification, but this was largely related to the disturbance of the OF buried bags by animals, which resulted in extremely high variability among OF plots. Other than that, there was a gradient of net nitrification of OF > TR = MW. There was no measurable nitrification in either inundated site (Figure 12). The pattern of daily rates of net mineralization was opposite that of net nitrification. Net mineralization was not significantly different between the TR and MW sites, but both were significantly and substantially higher in net mineralization than was OF (Figure 12).

Table 42
Nitrogen Data For Soils From Old-Field (OF), Transition (TR), and Mitigation-Wetland (MW) Sites

Site	NO_3^-, mg N/kg soil		NH_4^+, mg N/kg soil	
	Pre	Post	Pre	Post
OF	4.05 ± 0.14^b	5.61 ± 1.00^b	0.80 ± 0.20^c	1.16 ± 0.32^c
TR	5.66 ± 0.32^a	5.89 ± 0.53^b	6.53 ± 0.80^b	18.67 ± 1.81^b
MW	$5.39 \pm 0.26_b$	5.41 ± 0.22^a	23.50 ± 1.35^a	32.82 ± 2.17^a

Note: "Pre" and "post" refer to pre-incubation and post-incubation N values, respectively. Values shown are means of five transects ± one standard error of the mean. Means followed by the same superscript are not significantly different between sites at $p < 0.05$.

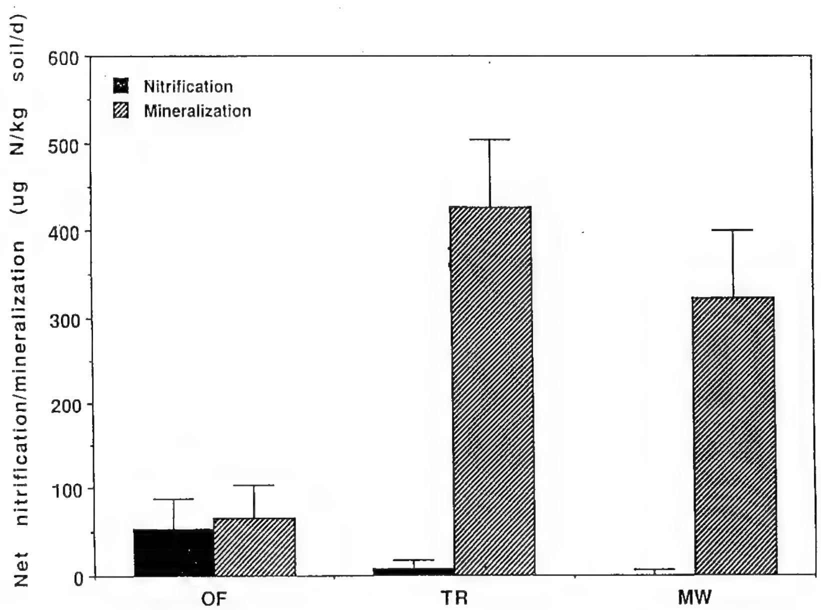


Figure 12. Net nitrification and mineralization of soils from three habitat types at GBWMA: old field (OF), transition (TR), and mitigation wetland (MW) (Values shown are means of five plots ± one standard error of the mean. Duncan's multiple range test showed no significant difference among site types for net nitrification. Means for net mineralization were not significantly different between TR and MW but were between OF and TR/MW at $p < 0.05$)

Study sites differed also in patterns in early growing season change in available N pools. Whereas available NO_3 did not change significantly from April to May on the TR and MW sites, there was a significant decrease in NO_3 on the OF site (Figure 13). In contrast to the seasonal pattern for NO_3, NH_4 increased significantly from April to May on the inundated sites but not on the OF site (Figure 14).

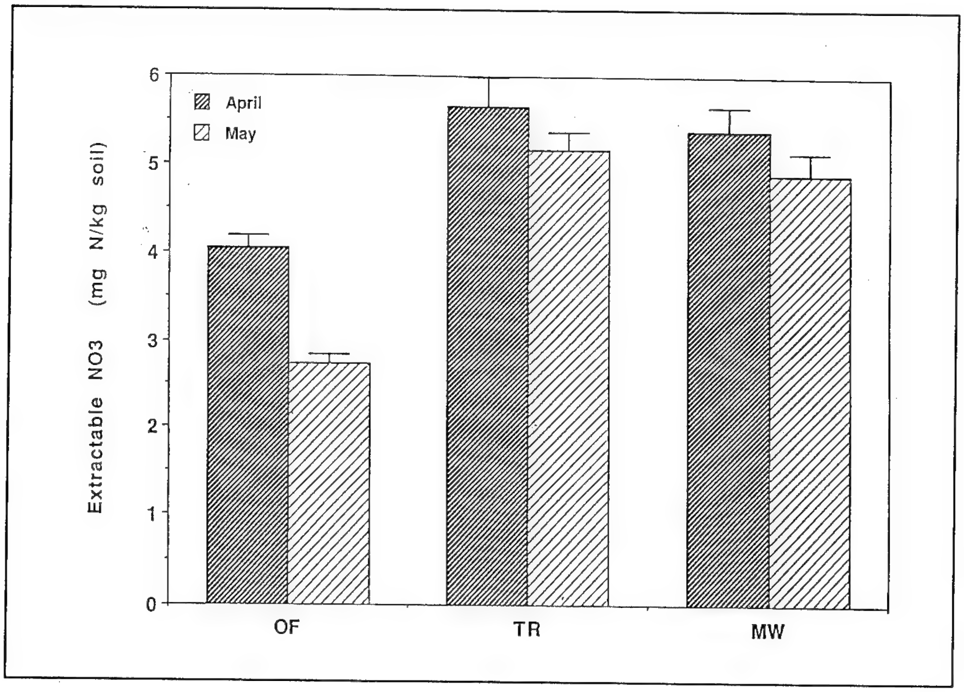


Figure 13. Extractable nitrate in April versus May for soils from three habitat types at GBWMA: old field (OF), transition (TR), and mitigation wetland (MW) (Values shown are means of five plots ± one standard error of the mean. Duncan's multiple range test showed no significant differences between TR and MW, but showed significant differences ($p < 0.05$) between OF and TR/MW. T-tests revealed a significant difference ($p < 0.0001$) between months for OF, but no differences between months for either TR or MW)

Discussion

Soil texture differences between the MW site and the other two sites (Table 41) were consistent with texture differences found between old-field soils and those of swamp sites within GBWMA (Gilliam 1993). It is not clear whether this was directly the result of the >1-year period of inundation for the MW soils, or perhaps an artifact of sampling conditions for water-logged soils. Sand particles themselves are quite stable under most conditions and should not break down in such a short period of time. However, tightly-bound clay aggregates which may behave as sand particles during hydrometric texture measurements might not be as stable under the prolonged reducing conditions of the mitigation wetland. Texture differences may also result from microtopographic gradients, wherein finer particles (silt and clay) settle out at lower positions during alluvial processes (Jenny 1980). Soil pH differences may also be responding to microtopography such that leaching and gravitational movement may bring base cations (especially Ca and Mg) to these lower positions. The large discrepancies between H_2O- versus KCl-extractable pH at all site

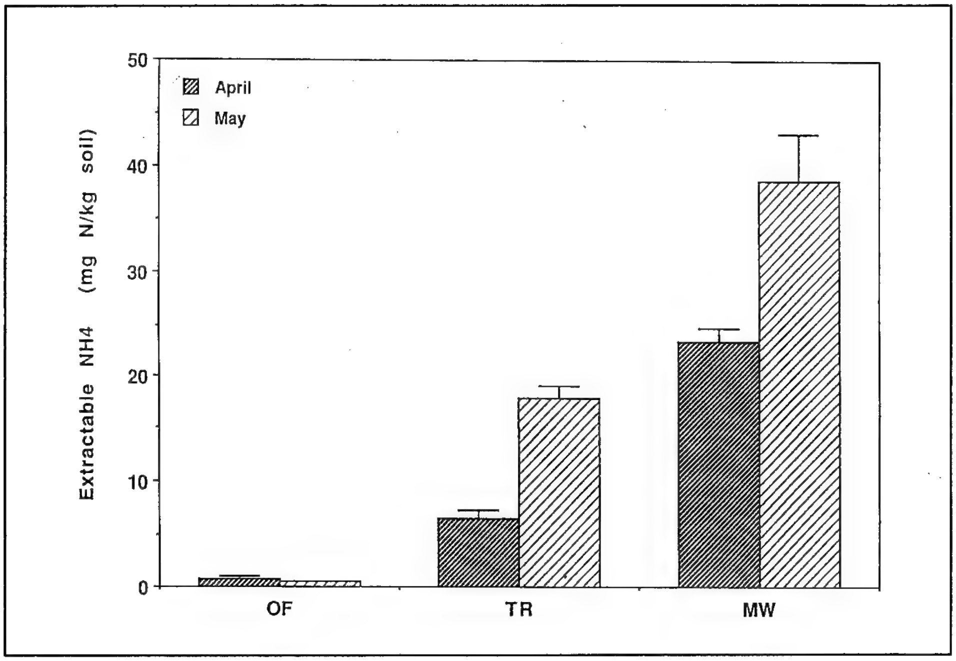


Figure 14. Extractable ammonium in April versus May for soils from three habitat types of GBWMA: old field (OF), transition (TR), and mitigation wetland (MW) (Values shown are means of five plots ± one standard error of the mean. Duncan's multiple range test showed significant differences among all sites (i.e., no site comparisons were nonsignificant at $p < 0.05$). T-tests revealed significant differences ($p < 0.05$) between months for TR and MW, but no difference between months for OF)

types suggests an appreciable amount of A1 and exchangeable acidity in soils of GBWMA (Gilliam 1991).

Regardless of site type, organic matter was somewhat low for these soils (Table 41), less than the 13.8 to 14.2-percent range reported for some West Virginia forests (Gilliam and Turrill 1993). The lack of significant differences between the OF site and the inundated sites is inconsistent with the results of Gilliam (1993), which found significant increases in soils following inundation. It was concluded that this increase resulted from increased detritus formation following rapid mortality under the anaerobic conditions of inundation.

The results of this study agree in general with conclusions of previous studies on the effects of inundation of the N fertility of old-field soils of GBWMA (Gilliam 1993). That study predicted that there will be a shift in the balance of available N from relatively equal amounts of NO_3 and NH_4 in the terrestrial soils of the old field toward increasing predominance of NH_4 as these soils approach a hydromorphic condition. Furthermore, it predicted an increase in pools of available N following inundation of terrestrial solid, predominantly (>99 percent) in the form of NH_4. A notable difference in the field and analytical approach taken by Gilliam (1993) and the present study is that the earlier study analyzed air-dried soils, whereas, this study extracted and

analyzed moist soils. Therefore, the similarities in conclusions of the two studies with different analytical conditions contradict conclusions of Gilliam and Richter (1985, 1988) who predicted that air-drying soils would have pronounced effects on extractable N and that this effect would be related to the redox status of the soil.

An additional difference between Gilliam (1993) and the present study is that by sampling only once at each sampling period (i.e., not incubating), N data from the earlier study presented only pools of N, not fluxes (e.g., mineralization, nitrification, microbial immobilization, and plant uptake). For example, it is possible that pools of N sampled at any one time are quite low as a result of rapid uptake of available N. Thus, N pools would be small, but N flux would be large.

Results of this study suggest that both pools and fluxes of available N vary substantially with the degree (time) of inundation. Although results of the ANOVA and Duncan's multiple range test revealed no significant differences among sites (Figure 12), this lack of significance was related to disturbance of the buried bags by animal activity. The net result was a greater variation of incubation conditions over the 28-day period and, consequently, greater variation in NO^2 production. Thus, it is concluded that nitrification is an important N transformation in OF soils. Other important components of N flux at the OF site would be microbial immobilization and plant uptake of NO_3 and NH_4. This would explain the seasonal decline in NO_3 (Figure 13) and the consistently low NH_4 at the OF site (Figure 14).

Patterns for NH_4 among the study sites form a clear gradient from OF to TR to MW, especially in examining seasonal pools (Figure 14). This suggests that mineralization is quite pronounced in all soils, but that, in the absence of aerobic processes driving N flux in old-field soils, NH_4 produced via mineralization accumulates under the anaerobic conditions of the TR and MW sites. This pattern is expected to change seasonally for the TR site as summer drawdown begins to re-expose these soils.

Conclusions

Results of this study generally support predictions of Gilliam (1993) concerning N transformations following inundation during mitigation-wetland creation. Results also support the idea that mitigation-area soils are developing toward true wetland (hydromorphic, *sensu* Buol and Rebertus 1988) soils after only ~1 year following inundation. Conditions in these soils are distinctly reducing, causing a significant change in the dynamics of N which are typical of hydromorphic soils (Mitsch and Gosselink 1993). Since N dynamics change rather rapidly following the creation of anaerobic conditions, more substantial changes in MW soils are not expected. In contrast, soils of the TR site, which will experience seasonal fluctuations in redox conditions, should exhibit similar seasonal patterns of change in N dynamics.

7 Bryophyte Communities[1]

Introduction

A wetland is defined as a vegetated or temporarily unvegetated area which is covered for at least several months of the year with less than 4 m of tidal water (Kirkpatrick and Harwood 1983). The water saturation level is the primary factor determining the type of soil substrate present and the plant and animal communities which inhabit the wetland (Cowardin et al., 1979). Wetlands are classified by the dominant vegetation present. For example, swamps are wetlands that are dominated by woody plants (trees and shrubs). These woody plants and other common swamp vegetation are adapted for survival in the aquatic environment. In turn, the dominant swamp vegetation directly influences the animal communities. Some of the swamp plant and animal communities can survive only in a hydric environment. Certain members of the divisions Hepatophyta and Bryophyta (liverworts and mosses) are common inhabitants of the hydric environment.

Because of their small size, simple morphylogy, and close proximity to the soil, liverworts and mosses are extremely sensitive to minor variations in habitat. Therefore, these organisms are superior indicators of their environment. If information concerning liverwort and moss community structure is available, the habitats of a wetland can generally be described.

The majority of swamp bryophytes are epiphytes on the bases of trees and shrubs. The other remaining small portion of the bryophyte population grows either on other tree parts (especially between the base and 1 m height), on saturated soil and on decaying logs which have fallen onto saturated soil, or into open water. Some swamp bryophytes are completely submerged in water for the major portion of the year.

Because of their preference for hydric conditions, wetland liverworts and mosses serve as pioneer species in the ongoing process of swamp succession. When these plants colonize partially submerged fallen logs and soil near the water's edge, the process reduces the open water areas of the wetland and provides a new substrate for the less hydric vegetation. Thus, the open areas

[1] Kimberly Cunningham, M.S.; Thomas E. Weaks, Ph.D.

of the wetland are in an earlier stage of succession than the densely vegetated areas. Likewise, the species diversity of an area is directly related to the area's successional stage. Since the open water areas are limited in substrate (trees and shrubs), only a few moss and liverwort species can colonize this aquatic environment. The densely vegetated areas containing a high number of substrate types can support a very diverse community of liverworts and mosses. Thus, by examining the species diversity of these plants in the various areas in the swamp, the stage of succession can be determined.

Probably the most important function of wetland liverworts and mosses is their role in the aquatic food chain. During most of the year, the main source of organic nutrition for many of the aquatic organisms (insects, fish, etc.) is the swamp's detritus. In the winter months, the detritus food source becomes less abundant. During this time, some aquatic organisms use the submerged liverworts and mosses as a food source. Submerged bryophytes also provide a substrate and protection for phytoplankton, periphyton, and insects (larval and adult stages). Without these valuable food resources, serious gaps in food chains may result.

Little is known about liverwort and moss communities of wetlands associated with the Ohio River. This paucity of information has resulted mainly in part from a failure of bryologists, who have conducted studies in the region, to recognize the important role these plants have in wetland ecosystems. The objectives of this study were to investigate the community structure of the bryophytes of GBWMA and to relate community structure to variations in environmental factors.

Literature Review

West Virginia liverwort and moss studies

Although mosses and liverworts are superb environmental indicators, studies of these plants are at a minimum in West Virginia (Englemann and Weaks 1985; and Weaks and Creekmore 1981). Only a few county (Ammons 1934) and state (Miller 1964) studies have been undertaken. The majority of new species were discovered by area-specific studies which investigated a particular problem and its effects on the bryophyte population (Weaks and Creekmore 1981; Englemann and Weaks 1985; Weaks et al. 1991; and Chaffin et al. In Press).

Only a few national, state, and county species lists have been compiled. Grout (1940) developed a list of continental moss species north of Mexico, and Stotler and Crandall-Stotler (1977) composed a North American liverwort and hornwort checklist.

Individual studies have been accumulated into several West Virginia and county species lists. Ammons (1934) compiled a list of West Virginian

mosses by combining Millspaugh's checklist with the herbarium collections of Sheldon, Gray, and Ammons. Wayne and Cabell County population data are not available from this list, as collection sites were not recorded. Ammons (1940) provided a manual of West Virginia liverworts which included a dichotomous key, detailed liverwort taxa descriptions, and sketches of each liverwort. Each species description consisted of morphologic features, reproductive information, habitat data, West Virginia counties of distribution, national occurrence, and distinguishing characteristics that aid in identification in the field.

According to Ammons (1934), twelve liverworts occurred in Wayne County, and six occurred in Cabell County. Three species, *Lophocolea heterophylla* (Schrad.) Dum., *Frullania squarrosa* (Reinw. et al.) Dum., and *Marchantia polymorpha* L., were found to occur in both counties.

A number of West Virginian liverworts and mosses have been reported in adjacent state studies. One Ohio liverwort study lists species which also occur in West Virginia, Pennsylvania, Kentucky, Michigan, and Indiana (Miller 1964).

Chaffin et al. (In Press), Weaks et al. (1991), Engelmann and Weaks (1985), and Weaks and Creekmore (1981) conducted area-specific liverwort and/or moss studies. Twenty-seven liverwort species were identified along a ravine near East Lynn Lake, Wayne County, WV (Chaffin et al. In Press). The study concentrated on the effects of flooding on the distribution of a stream's liverwort population and the usage of liverworts as disturbance indicators of erosion and flooding. Weaks et al. (1991) conducted an 18-habitat-type investigation in the Upper Shaver's Fork Basin, WV. Twenty-four hepatics and 109 mosses were identified in northern hardwood and spruce forests. In addition, rare species were identified, and species tolerance was evaluated. In the study of three Mingo county stream valleys, species diversity, heterogeneity, and equitability were compared for bryophyte communities (Engelmann and Weaks 1985). The study sites were representative of three successional stages: undisturbed land, land with on-going strip mining, and abandoned strip mine land. The results suggested that bryophytes, especially *Ceratodon purpureus* (Hedw.) Brid., could be used in the revegetation of abandoned strip mine land. A total of 97 moss species was found. Weaks and Creekmore (1981) investigated the effect of timbering on the distribution and diversity of hepatics. Twenty nonepiphytic and fifteen epiphytic hepatic species were observed at seven stations near Beech Fork Lake, Wayne County, WV.

Swamp species of liverworts and mosses

A study of Central Long Island's red maple swamp forest concentrated on swamp vegetation (Cain and Penfound 1938). Tree, shrub, and herb layers were sampled in five designated stations of the swamp forest. The bryophyte study listed the following data: moss and liverwort percent cover for each station, habitat (aquatic, wood peat, soil, and bark), dominant bryophyte

unions, tree species of moss inhabitation, cardinal points of moss distribution, height distribution on the tree, and bryophyte union successional relations.

The majority of swamp bryophyte information is obtained from county, state, and area studies (Clebsch 1974; Alteri and Coleman 1965; Redfearn and Halbert 1969; and West and Evans 1982). In these investigations, the study area was divided according to specific habitats (swamps, hummocks, and soil), and the bryophyte species found in each were listed. Swamp habitats were examined from the Kentucky-Tennessee area known as the Land Between the Lakes (Clebsch 1974). Nineteen swamp species of liverworts and mosses were found. Alteri and Coleman (1965) listed 44 species of woody swamp bryophytes in the Genesee County, Northern Wayne County, NY study. A seven-county study conducted in southern Michigan listed seventeen hardwood swamp species (Redfearn and Halbert 1969). West and Evans (1982) conducted an eight-site study along the lower Kanawha River Floodplain, two of which were swamp habitat (Winfield and Dunn's Swamps). Since the investigation concentrated on higher vegetation, limited bryophyte information was obtained. Ten bryophyte species were observed but were not identified. Only *Thuidium delicatulum* (L.) Mitt. was represented in the herbaceous plant list. *T. delicatulum* was present in Winfield Swamp but not in Dunn's Swamp.

Succession

Succession is a series of stages in which an area's community and its associated organisms are gradually replaced by the next community type until a stable community results (Brewer 1988). The general successional model moves through these five vegetation communities: annual herb, perennial herb, shrub, early forest, and climax forest (Brewer 1988). Because of the geographical location and the type of succession (wetland, bog, etc.), variations in the general model occur.

Information has been obtained on sand dune succession (Cowles 1899 and Shelford 1908) and bog succession (Brewer 1966 and Schwintzer 1979), but wetland succession information is limited. Because of an increased interest in the preservation of wetlands, Larson and Golet (1980) developed a successional model for wetlands. Open water, vegetated open water, deep marsh, shallow marsh, shrub swamp, and wooded wetland are the wetland's main successional stages (Larson and Golet 1980). In an effort to adapt this wetland model to a specific area, flood frequency, soil characteristics, species composition, and geographic location were examined (West and Evans 1982).

The stage of succession is a major influence on wetland species diversity. Vascular plant species diversity is highest in the annual grass wetland (deep marsh). From the stage, species diversity continually decreases, reaching a minimum in the wooded wetland stage (Evans 1975). Another factor influencing wetland species diversity is the water saturation level.

Submerged vegetational areas (which represent different successional stages) are dominated by one or two species (West and Evans 1982). A flora and early secondary succession study on the Lower Kanawha River Floodplain revealed that buttonbush (*Cephalanthus occidentalis* L.) or swamp rose (*Rosa palustris* Marsh.) dominate the shrub swamp (West and Evans 1982). Canary grass (*Phalaris arundinacea* L.) is the major species in the wet meadow; the main open water species are duckweeds [*Lemma minor* L. and *Spirodela polyrhiza* (L.) Schleid] or smartweeds (*Polygonum hydropiperoides* Michx.). Since these areas are limited to water-tolerant species, the diversity is low.

Successional development proceeds slowly in low diversity vegetation communities (Connell and Slatyer 1977). The open water and meadow stages must achieve a reduction in their water saturation level from permanently flooded to temporally flooded (Larson, Mueller, and MacConnell 1980). This is a longer process and a greater change than the replacement of the dominant species in the wooded wetland stage (Larson, Mueller, and MacConnell 1980).

Epiphyte succession

Autogenic succession is the colonization of available substrates in which the previous population has been removed by natural disturbance (Stone 1989). By controlling the surrounding microclimate conditions, these early species determine the length of their dominance.

Four models describing autogenic epiphyte succession have been developed. Clements' (1916) facilitation model suggests that pioneer species aid in secondary species growth by producing suitable habitat for later species and decreasing their own survival. On the other hand, Egler's (1954) initial floristic composition model predicts that secondary species cannot flourish until earlier species become extinct. This suggests that secondary community composition is highly dependent on the early community composition.

The initial floristic composition model has been further divided into two separate models (Connell and Slatyer 1977). In one of these, the tolerance model, pioneer species reduce their dominance by gradually lessening the availability of suitable habitat; thus, secondary species tolerant of this new microclimate prevail. In the second, the inhibition model, the early species create an environment in which no additional species can prevail.

Competition is a major influencing factor on succession (Stone 1989). Intraspecific competition is the main reason for pioneer species declining in the facilitation and tolerance models. In the inhibition model, early species are more strongly affected by predators, physical extremes, or local disturbance.

Stone's (1989) study of epiphytic succession on *Quercus quarryana* branches in the Willamette Valley, western Oregon, showed the earliest colonizing species to be lichens, especially *Usnea*. Mosses were among the secondary species appearing after 20 years. *Usnea* represents an inhibitor species

because of the combination of its ability to repress the growth of *Parmelia sulcata* Tayl. and *Melanelia subaurifera* (Nyl.) Essl. and its loss of dominance from predation (fungal parasites), physical conditions (rain and windstorms), and local disturbances (peeling bark). Two slow growing colonizers, *Parmelia sulcata* and *Orthotrichum lyellii* Hook. and Tayl., did not fit any of the models. Even though they facilitated the growth of other lichens and mosses, their presence was not necessary for the appearance of these secondary species.

The progression of epiphyte succession is determined by the integration of allogenic factors, facilitation, inhibition, and competition (Stone 1989). However, allogenic factors such as bark peeling and microclimate changes seem to be the most influential.

Relationships between moss, periphyton, and other organisms

Periphyton and microalgae are the preferred food source of certain aquatic herbivores (Van Montfrans, Wetzel, and Orth 1984). In the fall and winter months, the phytoplankton and periphyton populations decline (Weaks 1979). Thus, the aquatic organisms must resort to a secondary food source. Being primary producers, submerged mosses and liverworts may provide a portion of this needed nutrition (Glime and Action 1979). Since periphyton is a highly nutritious food source that is easily assimilated by herbivores (Brenner et al. 1976; Harrison 1977), this secondary food source (submerged mosses and liverworts) is not consumed unless the phytoplankton and periphyton communities are depleted.

In addition, these plants provide a valuable function in wetlands as a substrate for colonization by periphyton and other aquatic organisms (Glime and Clemons 1972).

Because aquatic bryophytes are usually ignored in ecological studies (Glime and Action 1979), limited information is available on the interrelationships of mosses and their associated periphyton. No studies concentrating on associations of periphyton and liverworts are available. Dealing indirectly with a moss-periphyton association, Glime and Action (1979) examined the effects of temperature and light intensity on the respiration rates of the *Fontinalis duriaei* (Schimp.) Husn.-periphyton association. The periphyton was not identified.

Information obtained from macrophyte-periphyton studies can be used to describe moss/liverwort-periphyton associations. Allen (1971) constructed a chemo-organotrophic model to describe this interdependent relationship. The model represents the metabolic interactions between the epiphyte (algae and bacteria) community and its submerged macrophyte. Allen's model establishes the chemical interrelationship but does not consider the macrophyte's influence on periphyton abundance and its distribution. As the macrophyte progresses through its life cycle, the surrounding water column is in a continuous state of change (Morin and Kimball 1983). Macrophyte growth results in a reduction in light availability, decreased water circulation, and water chemistry variation

(Morin and Kimball 1983). Thus, periphyton distribution and abundance are indirectly affected by the growth of the macrophyte. Morin and Kimball (1983) found that diatoms were the dominating periphyton species associated with the macrophyte *Myriophyllum heterophyllum* Michx. during early summer. In mid-summer, a successional periphyton distribution gradient occurred on *M. heterophyllum* Michx. The periphytes colonizing the lower stem region of the plant were diatoms with blue-greens and filamentous green algae dominating the upper stem. The upper stem environment was more suitable for the green and blue-green algae because of the higher concentrations of dissolved oxygen and higher light levels (Morin and Kimball 1983).

Macrophyte growth also indirectly affects population levels of epiphytes (Morin and Kimball 1983). Deteriorating leaves of the lower stem cause low periphyte populations because of a lack of an available substrate for colonization. Morin and Kimball (1983) found that lower and mid-stem periphyton populations remain stable, but apical elongation causes changes in epiphyte concentrations. The periphyton population is inversely related to apical elongation (Morin and Kimball 1983).

Herbivores can influence the rate of primary production and toxonomic structure of the algal community (Kehde and Wilhm 1972; Cooper 1973). Periphyton productivity usually increases as a result of grazing. Stewart (1987) found *Campostoma*, a minnow, increases the production rate as much as 200 to 250 percent. The increase in the production rate is due mostly to the removal of old and dead periphyton cells (Flint and Goldman 1975). Because of this herbivorous influence, interactions are created between the grazer, its algal food supply, and the periphyton's nutrient supply (Stewart 1987).

Most grazers add important nutrients to activate the primary productivity rate. Flint and Goldman (1975) found that crayfish introduce high levels of N (in the form of ammonia) into Lake Tahoe.

Many grazers are selective in the particular periphyton species they consume (Stewart 1987). The food source for each grazer is determined by its specific mouth parts (Allanson 1973). It was reported that the mayfly, *Cloeon*, dines on calcified periphyton because of the construction of its mouth parts.

Grazing has an important role in the food chain. If grazers are nonexistent, periphyton will overgrow and shade the host macrophyte limiting the amount of periphyton primary productivity (Taylor and Lewis 1970; Larkum 1976).

Niche structure of swamp bryophytes

The specific role served by a species is its niche (Gignac 1992). Two components comprise the species' overall niche: the fundamental and realized niche (Hutchinson 1957). The fundamental niche is the organism's entire habitat dictated by its individual tolerance to the surrounding environmental

factors. The species' realized niche is created when the fundamental niche is reduced by biotic factors such as predation, competition, and dispersal limitations.

Many studies have concentrated on the niche structure of bryophytes (Vitt and Slack 1984; Okland 1990; Slack 1990; McQueen 1991). The majority of these studies focused on mire bryophytes (Clymo 1973; Clymo and Reddaway 1974; Rydin 1985; Rydin and McDonald 1985; Gignac and Vitt 1990). Information gained from mire bryophyte niche structure studies can be used to explain the niche structure of swamp bryophytes, since both groups are wetland species.

An aquatic bryophyte's fundamental niche is determined by four environmental factors: local climate, shade, water chemistry, and height relative to the water table (Gignac 1992). Gignac's (1992) mire bryophyte-niche structure study concentrated on the influence these environmental factors have on total bryophyte, *Sphagnum,* and non-*sphagnum* distributions. When the total bryophyte population was considered, local climate proved to be the most influential factor; water chemistry and height from the water table were intermediate influences. Shade had an effect on the total bryophyte distribution. *Sphagnum* species had a similar ranking for the influential environmental factors. Water chemistry and shade had the least influence on distribution. However, the local gradients (water chemistry, shade, height relative to the water table) were more important in distinguishing the non-*Sphagnum* niches.

Interspecies competition is a major influence in creating a species-realized niche (Vitt and Slack 1984, Okland 1990). Habitat-specific species are better competitors than widespread species. In a hydric environment, the water-tolerant species are better equipped for survival. The competitive ability of these bryophytes is due to their structure. Lawn and carpet mosses are better adapted for survival in an aquatic habitat (Gignac 1992).

Bryologists use a niche shift as an indicator for interspecific competition (Haefner 1988). A niche shift occurs when widespread species become dominant due to the absence of habitat-specific species. Environmental factors such as local climate, rather than the absence of competition, cause some niche shifts.

Wilson and Keddy (1986) identified a competitive hierarchy which is apparent in wetland vascular plants. This strongly suggested the existence of a competitive hierarchy for aquatic bryophytes (swamp and mire).

Methods and Materials

Green Bottom Swamp is 80 ha in area, dominated by *Salix nigra* Marsh. and *Acer saccharium* Marsh., *Cephalanthus occidentalis* L., and *Hibiscus*

moscheutos. L. Liu (1991) constructed a seven-area map of the study site based on the dominant vascular vegetation (Figure 15). The original map was extended 200 m to the west of Area G to include an area along a creek (Area H).

Description of study areas

Area A - *Salix nigra-Acer saccharium* vegetation community. Located at the eastern end of the swamp (Figure 15), Area A is a well-developed swamp forest rich in vascular plant species. The average water saturation level is one of the lowest of the swamp (18.42 cm). The site is dominated by black willow (*Salix nigra*) in the tree layer, buttonbush *(Cephalanthus occidentalis)* in the shrub layer, and white grass (*Leersia virginica* Willd.) in the herb layer (Lui 1991).

Area B - *Salix nigra-Plantanus occidentalis* L. vegetation community. GBWMA contains two of these vegetation communities (Figure 15). The one at the eastern end of the swamp functions as a transitional zone between Areas A and C. The second is located at the western end. The average water depth is 39.80 cm. The dominant species are black willow *(Salix nigra)* in the tree layer and buttonbush *(Cephalanthus occidentalis)* in the shrub layer (Lui 1991). Since tree and shrub layers of Areas A and B are dominated by the same species, differentiating species of Area B should be noted. According to Lui (1991), Area B contains a higher coverage of duckweeds (*Lemma minor* L.) because of the higher water level. The two sites (A and B) are further separated by the presence of sycamore in Area B which are not found in Area A and the absence of rose and composite species from Area B that are present in Area A.

Area C - *Acer saccharinum-Plantanus occidentalis* vegetation community. The major portion of this community is located in the center of the swamp (Figure 15). The dominant species are *Acer saccharinum* and *Plantanus occidentalis* in the tree layer, *Cephalanthus occidentalis* in the shrub layer, *Saururus cernuus* L. in the herb layer, and *Lemma minor* in the open water (Lui 1991). The water saturation level averages 40.64 cm. The site is a wetland forest community with a high species richness and cover of floating plants and a lower species diversity in the shrub and herb layers. The three differentiating species are *Acer saccharinum* in the shrub layer, *Spirodela polyrhiza* (L.) Schleid. in the open water, and an absence of *Salix nigra* in the tree and shrub layers.

Area D - *Acer saccharinum-Salix nigra* vegetation community. The two sections of Area D form the boundary between the swamp and the surrounding fields (Figure 15). *Acer saccharinum* and *Salix nigra* dominate the tree layer while duckweed (*Lemma minor*) is the major species among the floating plants. Lui (1991) stated that the site was high in species richness especially in the herb layer. The average water depth is 50.80 cm. The presence of

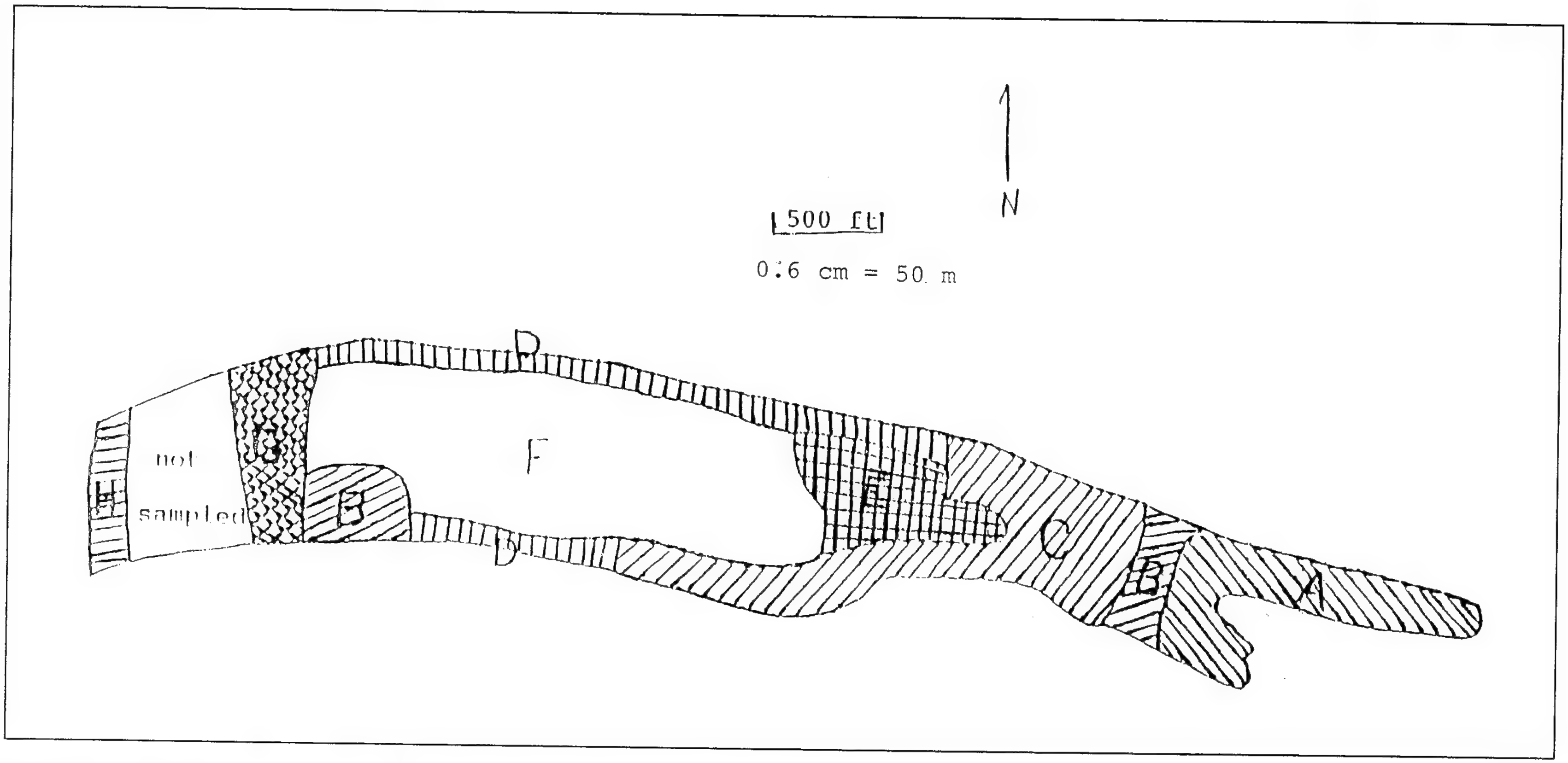


Figure 15. Vegetation map of GBWMA plant community (Adapted from Lui, 1991): (A) *Salix nigra-Acer saccharinum*, (B) *Salix nigra-Plantanus occidentalis*, (C) *Acer saccharinum-Plantanus occidentalis*, (D) *Acer saccharinum-Salix nigra*, (E) *Typha latifolia-Saururus cernuus*, (F) *Cephalanthus occidentalis*, (G) *Leersia oryzoides*, (H) *Salix nigra-Acer negundo*

Juncus effusus L. and *Polygonum coccineum* Muhl. separates this site from the other areas.

Area E - *Typha latifolia* L.-*Saururus cernuus* vegetation community. According to Lui (1991), this centrally located community is dominated by the common cattail (*Typha latifolia),* lizard's tail (*Saururus cernuus)* in the herb layer, and the floating plant, *Lemma minor* (Figure 15). Because of the lack of a tree layer and a low number of species in the shrub layer, Area E is representative of a wetland pasture successional stage. The water saturation level averages 63.50 cm.

Area F - *Cephalanthus occidentalis* vegetation community. Area F, located in the center of the swamp, is the largest of GBWMA's vegetation communities (Figure 15). Additionally, it has the highest water level (66.04 cm). Lui (1991) noted a high cover of buttonbush *Cephalanthus occidentalis* in the shrub layer, lizard's tail (*Saururus cernuus)* and marshmallow bushes (*Hibiscus moscheutos)* dominating the herb layer, and *Lemma minor* representing the main species among the floating plants. Species richness is low, due to the dense cover of buttonbushes.

Area G - *Leersia oryzoides* (L.) Sw. vegetation community. Rice cutgrass *(Leersia oryzoides)* and marshmallow bushes (*Hibiscus moscheutos)* are the main species of this community (Figure 15) (Lui 1991). Blockage of sunlight due to the high cover of the herb layer results in a low population of floating plants. The water level averages 46.56 cm. *Leersia oryzoides* is this community's dominant species.

Area H - *Salix nigra-Acer negundo* L. vegetation community. GBWMA's western most vegetation community is Area H - *Salix nigra* and *Acer negundo* (Figure 15). Since this area was not contained on Lui's (1991) vegetation map, the average water saturation level was not available. However, the water level is similar to Area A's (one of the lowest of the swamp). The vegetation community is dominated by *Salix nigra* and *Acer negundo* in the tree layer. The presence of *Acer negundo* can be used as the determinant species for this community.

Field survey

Lui's vegetation map (Figure 15) and a 25-m measuring line were used to establish the center of each community. From this point, a 50-m transect was set along either a east-west or north-south line, depending on the shape of the vegetation community. Ground bryophyte cover was established by centering a 20- by 20-cm grid over each meter mark on the transect line and calculating each bryophyte's total area (cm^2). Within 1 m of the transect line, tree bryophyte communities were sampled at cardinal points at a height of 1 m and at the tree base. To obtain the tree base cover, a 20- by 20-cm grid was centered on the bole with the lower surface resting on the ground. If the tree was surrounded by water, the grid's lower edge was placed at the surface of the water.

Directly 25 m to the north and south, other 50-m east-west transects were established. Coverage was calculated (area's individual bryophyte coverage (cm^2)/number of transects) for each species.

Disturbance values were assigned to each vegetation community. These values, ranging from one to six, were based on visual observations of the amount of disturbance to the canopy, understory, ground cover, soils, and drainage types.

Disturbance values were established as follows:

a. Undisturbed plant community.

b. Plant community with only minimal disturbance.

c. Mature trees present but evidence of disturbance in understory and ground cover.

d. Many young trees and grass present. No mature trees present.

e. Only a few saplings and no trees present.

f. High degree of soil disturbance. Grasses covering only a small area.

Laboratory analysis

Nomenclature for mosses follows Crum and Anderson (1981) and for liverworts, Stotler and Crandall-Stotler (1977). A complete set of vouchers has been deposited in the MUHW, Huntington, WV.

Computer analysis of data

Moss and liverwort species diversity is the combination of three factors: species richness, heterogeneity, and equitability (Engelmann 1980). Differences among vegetation communities were evaluated by considering the interrelationship of these three factors. Species richness is the number of moss/liverwort species in a designated community. Thus, the community with the highest number of species is considered the most advanced on the successional scale.

Slack (1977) proposed that total coverage rather than individual plants is the most concise means of measurement of mosses and liverworts because of moss and liverwort mostly colonial growth patterns. Therefore, total cover was used in the calculation of Equations 1-10.

The second factor, heterogeneity, is a more complex measurement than species richness. Simpson's heterogeneity distinguishes changes in the most

common species of the area (Peet 1974). The index is represented by the following formula:

$$HETEROGENEITY\ (Simpson's) = 1 - \Sigma \left[\frac{n_i(n_i-1)}{N(N-1)} \right] \tag{1}$$

where

n_i = number of individuals in taxa i

N = total coverage of all species in the sample

The highest heterogeneity ratio contains the highest number of the most common species. If this test is used separately, the most advanced successional community is the one containing the highest total coverage of the most common species.

The last factor, equitability, reflects the evenness of the moss/liverwort population (Pielou 1974). The vegetation community with the highest equitability has the highest even coverage between moss and liverwort species. Pielou's (1974) equitability is calculated using the following formula:

$$J' = \frac{H'}{Log(S)} \tag{2}$$

where

H' = the Shannon-Weaver Index

S = the total number of taxa

The Shannon-Weaver Index differs slightly from the diversity device (combination of richness, heterogeneity, and equitability) previously discussed. The Shannon-Weaver Diversity Index (H') (1963) concentrates on the combination of species richness and evenness. This formula has the following mathematical representation:

$$H' = \Sigma\ (p_i)(\log\ p_i) \tag{3}$$

where p = proportion of the total in the i^{th}.

Heterogeneity, which focuses on the most common species, is not incorporated in this formula. This index detects the rare species of the vegetation community (Peet 1974). Thus, the vegetation community with the majority of species evenly distributed would have the highest diversity and would be representative of the most advanced stage of succession.

These three formerly mentioned factors (species richness, heterogeneity, and equitability) emphasize different aspects to evaluate the community. Using a combination of these factors provides a precise description of the vegetation community and accurate identification of the stage of succession.

The following four formulas are used for making comparisons of vegetation communities or specific variables (water depth, equitability, etc.) of communities. The first of these, Sorensen's quotient of similarity, (*QS*), is used to evaluate cover similarities between two communities (Slack 1977). The QS equation is as follows:

$$QS = \frac{2C}{S1 + S2} \tag{4}$$

where

C = number of species in both communities

$S1$ = number of species in community 1

$S2$ = number of species in community 2

Thus, two communities having equal coverage of the same species will result in a high QS. This indicates that the two communities are identical and are in the same stage of succession.

The multiple community similarity, Jaccard Coefficient (*JC*), is a second means of comparing two communities. The following equation is used to calculate multiple community similarity:

$$JC = \frac{C}{S1 + S2 - C} \tag{5}$$

where

C = number of species in both communities

$S1$ = number of species in community 1

$S2$ = number of species in community 2

The multiple community similarity and Sorensen's QS obtain similar results, except that *JC* ratios are slightly lower than *QS*. Because of this difference in these two formulas, the *JC* index concentrates more on the presence and absence of data (number of taxa in both communities). Comparison of the *JC* and the *QS* formulas suggests that the absence of the coefficient 2 preceding the C in the numerator in the *JC* equation is the more probable reason for these lower values, instead of the $-C$ in its denominator. Even with this slight difference in the equation, two communities with an equal number of the same species of mosses/liverworts will have the same multiple community similarity ratio and will be in the same stage of the successional process.

The last two types of data analysis are statistical tests used to compare specific aspects (water depth, equitability, heterogeneity, number of species, etc.) of different vegetation communities. Linear regression is used to evaluate the degree of correlation between two specific aspects of vegetation communities. Represented below is the linear regression model (Neter, Wasserman, and Kutner 1990):

$$Y_i = B_0 + B_1 X_i + E_i \tag{6}$$

where

Y_i = the value of the response variable in the i^{th} trial

B_0 = y intercept of the linear regression line

B_1 = slope of the linear regression line

X_i = a known constant - the value of the independent variable in the i^{th} trial

E_i = random error term

To interpret data using linear regression, the coefficients B_0 and B_1 must first be determined. These coefficients are calculated using the moss/liverwort field data. B_1 is the slope of the regression line; the y-intercept of this line is represented by B_0. Formulas for calculating these two coefficients are as follows:

$$B_1 = \frac{\Sigma X_i Y_i - \Sigma X_i \Sigma Y_i/n}{\Sigma X_i^2 - (\Sigma X_i)^2/n} \tag{7}$$

where n = number of individuals in taxa.

The slope (B_1) is used to describe the relationship between the two specific aspects. For example, a negative slope representing a comparison between water depth and number of species suggests that as the depth of the water decreases, the number of species increases (indirect correlation). A positive slope results in a direct correlation, meaning that as one variable increases, so does the second.

A secondary statistical test usually performed in association with linear regression is the calculation of the correlation coefficient. The correlation coefficient (r) determines the degree of correlation between the two moss/liverwort aspects being compared by linear regression. The correlation coefficient (r) can be calculated by applying the moss/liverwort aspects (water depth, heterogeneity, etc.) to the following formula (Neter, Wasserman, and Kutner 1990):

$$r = \frac{\Sigma X_i Y_i - (\Sigma X_i \Sigma Y_i)/n}{\left\{\left[\Sigma X_i^2 - \left(\frac{\Sigma X_i^2}{n}\right)^2\right]\left[\Sigma Y_i^2 - \left(\frac{\Sigma Y_i}{n}\right)^2\right]\right\}^{1/2}} \tag{8}$$

The closer the value is to one, the stronger the correlation between the two variables. Linear regression and the correlation coefficient were used to detect the interrelationship between coverage and heterogeneity, disturbance and heterogeneity, and water depth and species diversity. The successional stage of the vegetation communities can be used to determine the most influencing aspects on the current stage of succession.

The last form of analysis, step-wise linear regression, determines which moss/liverwort aspects are the most influential on the other aspects. Four aspects (number of species, diversity, equitability, and heterogeneity) were tested to identify the most influential aspect and were incorporated into the regression model. Initially, the regression model has no X values (Neter, Wasserman, and Kutner 1990):

$$Y_i = B_0 + E_i \tag{9}$$

where

Y_i = the value of the response variable in the i^{th} trial

B_0 = the y-intercept of the regression line

E_i = the random error term

The X values are added based on their F values. The first variable incorporated into the model is by choice. If the F-calculated value containing this chosen value is higher than the F table value, then the next X variable is added. X variables are added until the calculated F no longer exceeds the table F value*. The process is repeated until all four aspects have been the chosen variable. Each linear regression has an associated correlation coefficient which determines the extent of the correlation. The regression with the highest correlation coefficient is the preferred model. Thus, the most influential aspects can be determined by observing which variables are present in the preferred model (Neter, Wasserman, and Kutner 1990). By interpreting the combination of these most influential aspects, one can obtain the best estimate for the exact point of succession.

$$F_k^* = \frac{MSR\ (X_k)}{MSE\ (X_k)} \tag{10}$$

where

MSR = mean squared regression coefficient of the specific aspect

X_k = a known constant - the value of the independent variable in the k^{th} trial

MSE = mean squared error of the specific aspect

Results

Twenty-five moss species and four liverwort species were observed at GBWMA (Tables 43 and 44). The dominant mosses for the area were *Amblystegium riparium* (Hedw.) BSG, *Amblystegium serpens* (Hedw.) BSG, and *Haplocladium virginianum* (Brid.) Broth. (Table 45). *Riccia fluitans* L. and *Frullania inflata* Gott. were the dominant liverwort species.

The moss with the highest coverage, *Amblystegium riparium,* was present in all vegetation communities except Area G (Table 45). *Amblystegium serpens* and *Haplocladium virginianum* occurred in only two vegetation communities.

Table 43
Moss Species Occurring at GBWMA

Kingdom Planta
Phylum Bryophyta
Subdivision Musci
Class Bryosida
Subclass Bryidae
Order Dicranales
Family Dicranaceae
Bruchia Schwaegr.
Dicranella heteromalla (Hedw.) Schimp.
Dicranum montanum Hedw.
Order Pottiales
Family Pottiaceae
Subfamily Trichostomoideae
Desmatodon Brid.
Desmatodon porteri James ex Aust.
Order Funariales
Family Ephemeraceae
Micromitrium austinii Aust.
Order Bryales
Family Mniaceae
Mnium hornum Hedw.
Mnium cuspidatum Hedw.
Order Hypnobryales
Family Fabroniaceae
Anacamptodon sphlachnoides (Froel. ex Brid.) Brid.
Family Leskeaceae
Anomodon attenuatus (Hedw.) Hub.
Anomodon minor (Hedw.) Furnr.
Family Thuidiaceae
Haplocladium virginianum (Brid.) Broth.
Family Amplystegiaceae
Amblystegium tenax (Hedw.) C. Jens.
Amblystegium varium (Hedw.) Lindb.
Amblystegium serpens (Hedw.) BSG
Amblystegium riparium (Hedw.) BSG
Family Brachytheciaceae
Brachythecium acuminatum (Hedw.) Aust.
Brachythecium oxycladon (Brid.) Jaeg. & Sauerb.
Rhynchostegium serrulatum (Hedw.) Jaeg. & Sauerb
Eurhynchium hians (Hedw.) Sande-Lac.
Family Entodontaceae
Entodon compressus C.M.
Entodon brevisetus (Hook. & Wils. ex Wils.) Lindb.
Entodon cladorrhizans (Hedw.) C.M.
Family Hypnaceae
Platydictya subtile (Hedw.) Crum.
Taxiphyllum taxirameum (Mitt.) Fl.

Amblystegium serpens was found in Area A (*Salix nigra* Marsh.-*Acer saccharinum* Marsh.) and Area D (*Acer saccharinum-Salix nigra). Haplocladium virginianum* was present in Area A (*Salix nigra-Acer saccharinum)* and Area H (*Salix nigra-Acer negundo* L.). However, the total coverage of the liverwort species was not directly proportional to the number of areas they inhabit. *Riccia fluitans* was found in three vegetation communities [Area A - *Salix nigra-Acer saccharinum*, Area D - *Acer saccharinum-Salix nigra,* and

Table 44
Liverwort Species Occurring at GBWMA

Kingdom Planta
Phylum Bryophyta
Class Hepaticae
Order Jungermanniales
Family Lophocoleaceae
Lophocolea minor Nees
Family Jubulaceae
Frullania inflata Gott.
Order Marchantiales
Family Ricciaceae
Ricciocarpus natans (L.) Corda.
Riccia fluitans L.

Area G - *Leersia oryzoides* (L.) Sw.]. *Frullania inflata* was present in four communities (Area A - *Salix nigra-Acer saccharinum*; Area B - *Salix nigra-Plantanus occidentalis* L.; Area C - *Acer saccharinum-Plantanus occidentalis;* and Area H - *Salix nigra-Acer negundo).*

Moss and liverwort families were examined to determine which had the highest species richness and coverage. Two families (Amplystegiaceae and Brachytheciaceae) contained the highest number of moss species (4 species) (Table 43). The highest moss cover was observed for the family Amblystegiaceae (9,597.98 cm^2) (Table 45). The Ricciaceae represented the family with the highest liverwort coverage and number of species (Table 44).

Species diversity is a function of species richness, equitability, and heterogeneity. The *Salix nigra-Acer saccharinum* vegetation community (Area A), with 13 species, had the highest species richness (Table 45). Area H (*Salix nigra-Acer negundo* vegetation community) had the second highest with 9 species. Two vegetation communities, *Typha latifolia* L.-*Saururus cernuus* L. (Area E) and *Cephalanthus occidentalis* L. (Area F), had the lowest species richness.

The highest equitability ratios were for *Leersia oryzoides* and *Acer saccharinum-Salix nigra* vegetation communities (G = 0.890; D = 0.859) (Table 46). The three highest heterogeneity values were Area H (*Salix nigra-Acer negundo)* (0.774), Area A (*Salix nigra-Acer Saccharinum)* (0.769), and Area D (*Acer saccharinum-Salix nigra)* (0.758) (Table 46). The *Salix nigra-Plantanus occidentalis* and the *Leersia oryzoides* vegetation communities had similar heterogeneities (B = 0.439, G = 0.452). A successional representation of the vegetation communities indicated that heterogeneity increased as succession progressed (Figure 16). Equitability increased in every successional direction, except in the westward direction (Figure 16).

The QS was used to compare the eight vegetation communities. The highest ratio, 1.000, was obtained when comparing Area E - *Typha latifolia-Saururus cernuus* and Area F - *Cephalanthus occidentalis,* since both

Table 45
Moss and Liverwort Cover for Eight Vegetation Communities at GBWMA

Species	Community Types							
	A	B	C	D	E	F	G	H
Mosses								
A. riparium	889	34	1,352	64	2,855	3,448	0	179
A. serpens	590	0	0	165	0	0	0	0
A. tenax	0	0	0	0	0	0	0	1
A. varium	22	0	0	0	0	0	0	0
A. sphlachnoides	21	0	0	142	0	0	0	0
A. attenuatus	6	0	0	0	0	0	0	0
A. minor	0	0	0	0	0	0	0	382
B. acuminatum	0	0	0	32	0	0	0	0
Desmatodon	0	0	0	0	0	0	0	1
E. brevisetus	0	0	0	0	0	0	0	42
E. compressus	0	0	0	80	0	0	0	0
E. cladorrhizans	181	0	40	0	0	0	0	0
H. virginianum	408	0	0	0	0	0	0	107
M. cuspidatum	0	0	0	0	0	0	0	14
P. subtile	0	24	0	0	0	0	0	0
R. surrulatum	8	0	0	0	0	0	0	0
T. taxirameum	6	0	0	0	0	0	0	184
Liverworts								
F. inflata	3	160	2	0	0	0	0	120
R. natans	10	0	0	0	0	0	5	0
R. fluitans	376	0	0	10	0	0	12	0

Note: Values are for Cover (cm^2).

contained the same species (*Amblystegium riparium*) (Table 47). Area B - *Salix nigra-Plantanus occidentalis* and Area C - *Acer saccharinum-Plantanus occidentalis* had the second highest QS (0.571). The majority of the QS ranged between 0.300 and 0.400 (Table 47). The ratio of 0.133 [Area D (*Acer saccharinum-Salix nigra)* and Area H (*Salix nigra-Acer negundo)*] was the lowest, except for the community comparisons that were 0 percent. The majority of vegetation communities where QS = 0 were for Areas E or F.

Table 46
Heterogeneity and Equitability Ratios for Eight Distinct Vegetation Communities

Vegetation Communities	Heterogeneity (Simpson's)	Equitability (Pielou's)
A	0.769	0.644
B	0.439	0.624
C	0.058	0.126
D	0.758	0.859
E	0.000	0.000
F	0.000	0.000
G	0.452	0.890
H	0.774	0.755

Note: Heterogeneity was calculated using Simpson's formula, and Pielou's formula was used to calculate equitability.

The JC identifies vegetation communities which are similar in their moss and liverwort coverage. The QS (Table 49) and JC (Table 48) were the same (1.000) for Area E (*Typha latifolia-Saururus cernuus*) compared with Area F (*Cephalanthus occidentalis*). The other pairs' percentages were slightly lower than the ratios for QS. Area B (*Salix nigra-Plantanus occidentalis*) and Area A (*Salix nigra-Acer saccharinum*) were second highest (0.400) (Table 48). The majority of the similarity ratios ranged between 20 and 30 percent. Five community pairs had a ratio between 0.100 and 0.200. As with the QS, Area A (*Salix nigra-Acer saccharinum*)/Area E (*Typha latifolia-Saururus cernuus*) and Area A/Area F (*Cephalanthus occidentalis*) had the highest value (0.077) (Table 48). With a ratio of 0.071, Area D (*Acer saccharinum-Salix nigra*)/ Area H (*Salix nigra-Acer negundo*) had the lowest value except for the 0 percent pairs (Table 48).

Using correlation/regression analysis, the disturbance values (x axis) of each vegetation community were compared with its diversity (Simpson's heterogeneity ratio) (y value) (Figure 17). Interpretation of the slope of the line and use of the coefficient of correlation, the amount of an area's disturbance has in influencing its diversity, was evaluated. The slope (-0.268) of the regression line indicates that the disturbance and the diversity of a community are indirectly proportional. Thus, the lower the disturbance level, the higher the diversity. For example, the disturbance value of three for Area A (*Salix nigra-Acer saccharinum*) was low, and its species diversity was high (0.769). The coefficient of correlation (-0.708) suggests that diversity and the disturbance of an area are strongly correlated (Figure 17). Therefore, the diversity is highly influenced by the degree of disturbance.

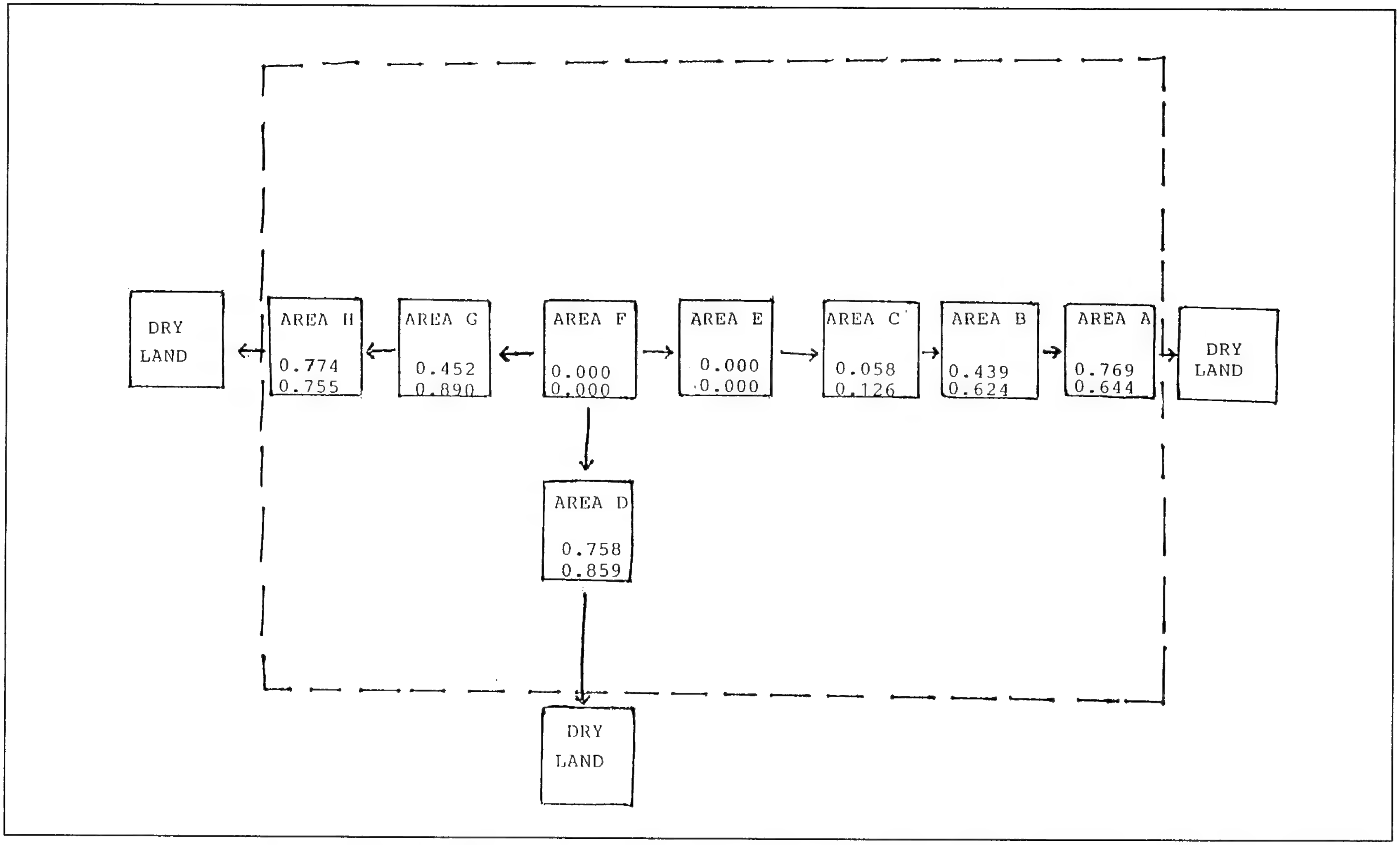


Figure 16. Relationship of each vegetation community's heterogeneity and equitability ratios to wetland succession (Top values represent each community's heterogeneity ratio, and the bottom value is the equitability representation. Arrows depict successional trends)

Table 47
Quotient of Similarity Ratios for Eight Distinct Vegetation Communities

Vegetation Community	A	B	C	D	E	F	G	H
A	0.000							
B	0.353	0.000						
C	0.375	0.571	0.000					
D	0.421	0.200	0.222	0.000				
E	0.143	0.400	0.000	0.000	0.000			
F	0.143	0.400	0.000	0.000	1.000	0.000		
G	0.267	0.000	0.000	0.250	0.000	0.000	0.000	
H	0.364	0.308	0.333	0.133	0.000	0.000	0.000	0.000

Note: Calculations were performed using Sorensen's index.

Table 48
Multiple Community Similarities Values for Eight Vegetation Communities

Vegetation Community	1	2	3	4	5	6	7	8
1	0.000							
2	0.214	0.000						
3	0.231	0.400	0.000					
4	0.267	0.111	0.125	0.000				
5	0.077	0.250	0.000	0.000	0.000			
6	0.077	0.250	0.000	0.000	1.000	0.000		
7	0.154	0.000	0.000	0.143	0.000	0.000	0.000	
8	0.222	0.182	0.200	0.071	0.000	0.000	0.000	0.000

Note: Calculations were obtained using the Jaccard index.

A second comparison was performed to evaluate the influence that water level has on the heterogeneity of each vegetation area. An indirect relationship exists between water depth and heterogeneity, represented by a slope of -1.350×10^{-2} (Figure 18). When the water saturation level was high, the heterogeneity value was low. For example, Area F (*Cephalanthus occidentalis)* had the highest water depth (66.04 cm) and the lowest heterogeneity ratio (0.000). Area D (*Acer saccharinum-Salix nigra)* was the one exception

Table 49
Evaluation of the Factors that Influence Succession

Regression Models	Correlation Coefficient (r)
1. $X_1 = X_2$	0.879
2. $X_2 = X_4 + X_3$	0.999
3. $X_3 = X_4 + X_2$	0.989
4. $X_4 = X_2 + X_3$	0.999

Note: Factors analyzed were species richness (X_1), species diversity (X_2), equitability (X_3), and heterogeneity (X_4).

with the third highest water depth (50.80 cm) and the third highest heterogeneity value (0.758). The associated coefficient of correlation (r = -0.766) (Figure 18) indicates a strong interrelationship between water depth and heterogeneity.

The influence of each community's total moss/liverwort cover on its heterogeneity was determined using linear regression and its associated correlation coefficient (Figure 19). The slope (-1.34×10^{-4}) (Figure 19) demonstrates an indirect relationship between cover and heterogeneity. When the cover is high, the heterogeneity is low. However, only an intermediate relationship exists between cover and heterogeneity (r = -0.499) (Figure 19). Thus, a vegetation community's total moss/liverwort cover does not greatly influence its heterogeneity.

The final statistical test, step-wise linear regression, was used to establish the most important aspect. Completed regression models 2, 3, and 4 have high r values of 0.998, 0.989, and 0.999, respectively (Table 49). Each of these models contains the same three aspects (diversity, equitability, and heterogeneity. Completed model 1 had a correlation coefficient value of 0.879 (Table 49), showing that species richness only slightly influences diversity. Thus, a strong interrelationship exists among diversity, equitability, and heterogeneity. The specific point of succession can be more appropriately estimated by using a combination of diversity, equitability, and heterogeneity data.

Discussion

Highest moss cover was for the family Amblystegiaceae. Highest cover was for the families Brachytheciaceae and Amblystegiaceae. According to Conrad and Redfearn (1979), the majority of Amblystegiaceae species are found on soil or rocks near water. Brachytheciaceae species usually inhabit soil, rocks, tree bases, and logs (Conrad and Redfearn 1979). The high success of these two families is probably due to the presence of extensive suitable

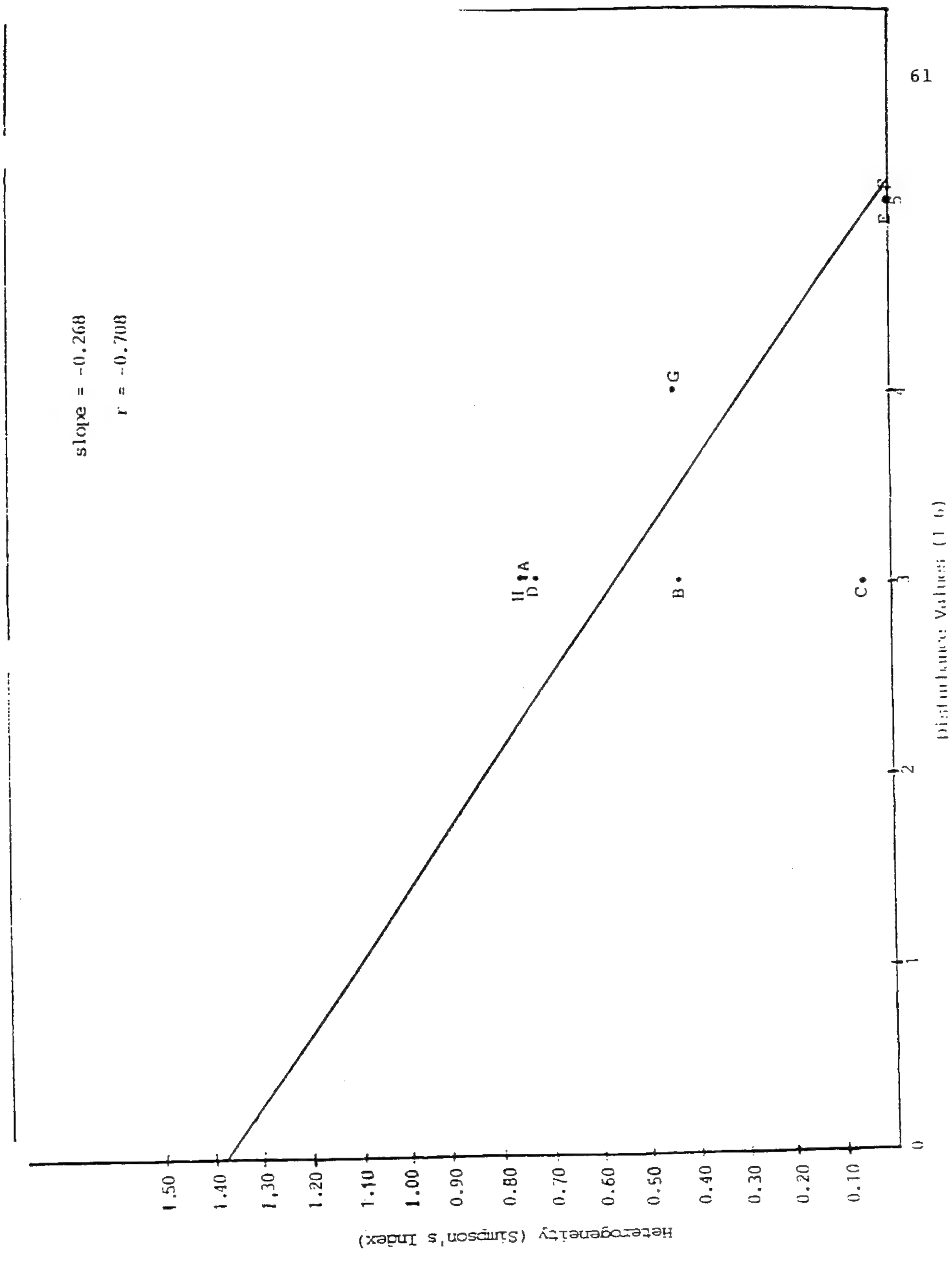


Figure 17. The effect of the disturbance level of each vegetation community on its heterogeneity ratio

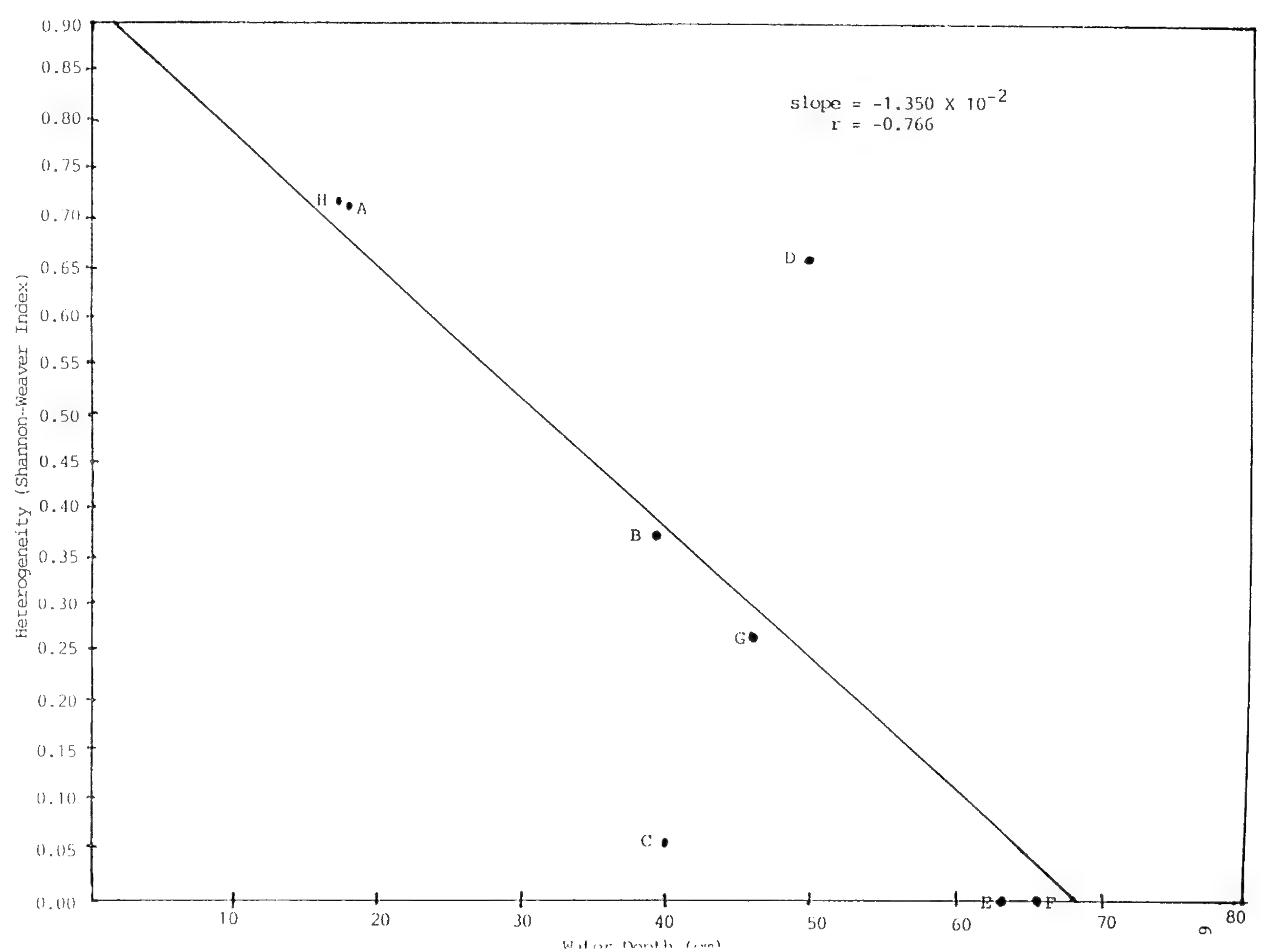


Figure 18. The effect of the water depth on the vegetation community's heterogeneity

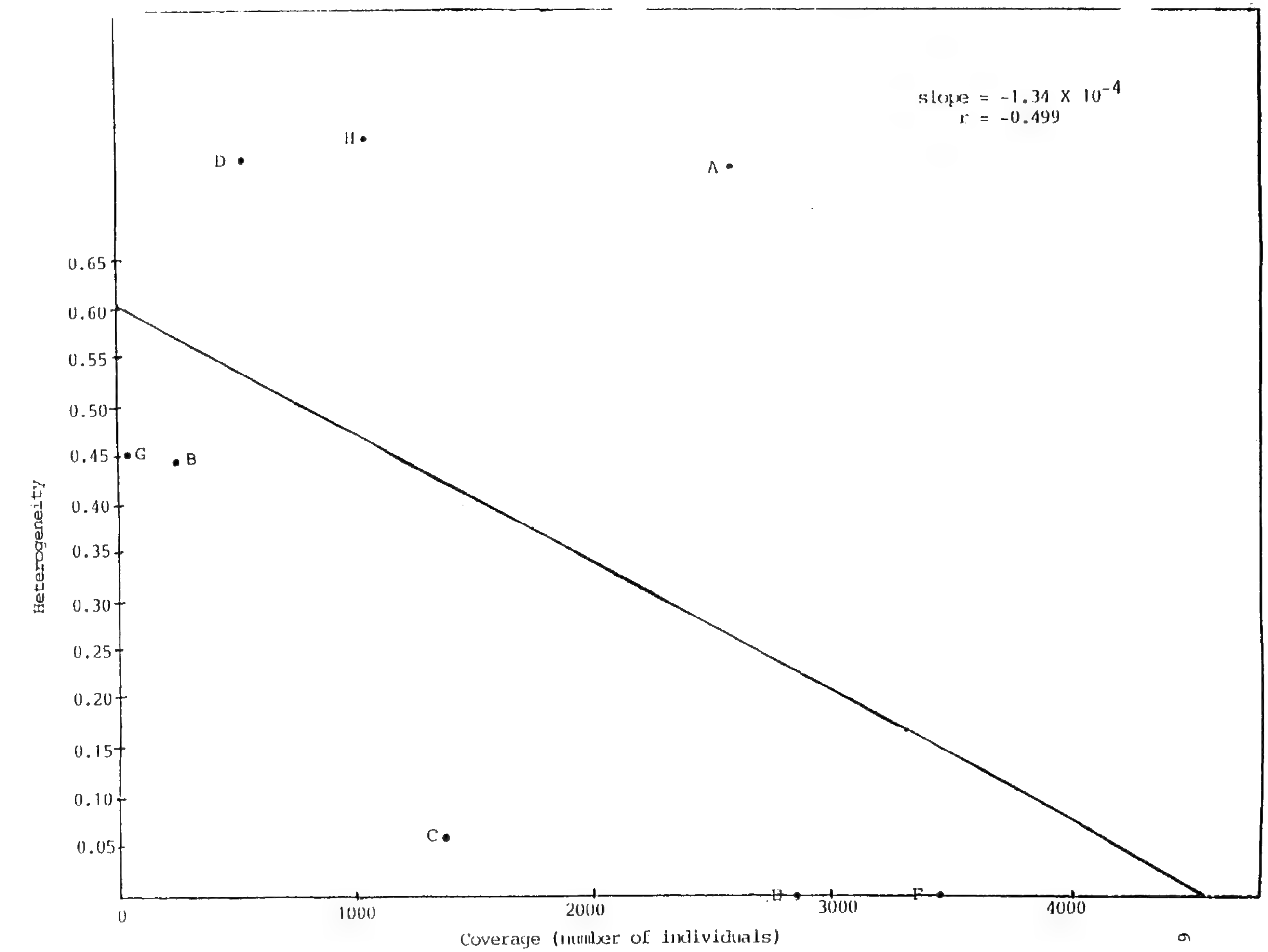


Figure 19. The effect of the bryophyte coverage of each vegetation community with its heterogeneity value

habitats at GBWMA. Bryophyte habitat is a function of four environmental factors: local climate, shade, water chemistry, and height relative to the water table (Gignac 1992). Species of the Amblystegiaceae had a much higher total cover than Brachytheciaceae even though they had the same number of species. Because the Amblystegiaceae species prefer a more hydric environment, wetlands of the study area were more favorable for Amblystegiaceae species than for Brachytheciaceae species. Gignac (1992) observed that habitat-specific bryophyte species are better competitors than widespread species.

Damp soil is the typical habitat for members of the family Ricciaceae (Conrad and Redfearn 1979). The study area's various water saturation levels provide excellent habitat for these species.

The two mosses, *(Amblystegium riparium* (Hedw.) BSG and *Amblystegium serpens* (Hedw.) BSG, were the species with the highest coverage and species richness. *Amblystegium riparium* is a robust green-yellow plant growing in loose, flat mats on humus twigs, branches, roots, and rocks in wet places inundated by flowing water (Conrad and Redfearn 1979). *Amblystegium serpens* is a small yellowish-green plant growing on moist soil, humus, and wood in wet habitats. Since the majority of the study area's vegetation communities is either forested or swampy, the dominance of these two species is probably related to the high availability of suitable substrates. *Haplocladium virginianum* (Brid.) Broth., another dominant moss, is a member of the family Thuidiaceae. These dark green plants grow in tangled mats on the soil or rocks (Conrad and Redfearn 1979). Only two of the study areas (A and H) contain soil which is not totally submerged; therefore, these are the only communities capable of supporting this species. The habitat availability is much greater for the two *Amblystegium* species than for *Haplocladium virginianum*. This is believed to be directly related to the dominance of *Amblystegium* spp.

The dominant liverwort, *Riccia fluitans* L., is a member of Ricciaceae, the family highest in total cover and number of species. According to Conrad and Redfearn (1979), *Riccia fluitans* occurs as a tangled mass either floating or on damp soil. *Frullania inflata* Gott., the species with the second highest cover, is a member of the family Jubulaceae. This dull green liverwort grows intermingled with other bryophytes in loose tufts on rocks and trees (Conrad and Redfearn 1979). Because of differences in their habitat preference, different successional niches are probably filled by these two species.

If leaf sizes of moss species are approximately equal, the difference in coverage must be directly related to the number of vegetation communities which they inhabit (Conrad and Redfearn 1979). For example, *Amblystegium riparium,* the species of highest cover, was present in seven of the eight vegetation areas. Its high occurrence must be, at least in part, the reason for high cover. Habitat-specific bryophyte species are better competitors than widespread species (Gignac 1992). However, the species with the second highest cover, *Amblystegium serpens* and *Haplocladium virginianum,* colonized only two communities. *Amblystegium serpens* had a slightly larger cover than *Haplocladium virginianum,* indicating yet another possible factor influencing

the colonization of substrates. It seemed reasonable to assume that the number of communities inhabitated by a particular species is directly related to the availability of suitable substrates.

The leaf size of the liverwort, *Frullania inflata,* is somewhat less than that for *Riccia fluitans* (Conrad and Redfearn 1979). In the present study, *Frullania inflata* occurred in fewer vegetation areas than *Riccia fluitans*. This suggests that liverwort leaf size is a more important factor in establishing total cover than in regulating the colonization of vegetation communities.

By examining the distribution of the mosses and liverworts, the successional progress of GBWMA's vegetation communities can be more clearly elucidated. The bryophyte communities present suggest that the eight vegetation areas are in distinctly different stages of succession. In addition, each area's stage can be roughly identified by its vascular vegetation. Wetlands communities pass through the following series of successional stages: open water, vegetated open water, deep marsh, shallow marsh, shrub swamp, and wooded wetland (Larson and Golet 1980). The majority of the vegetation communities studied are of the wetland successional stage (Areas A, B, C, D, and H). Even though these communities may appear to be in approximately the same successional stage, they undoubtedly differ in the degree of progression required to reach the end point of succession. The water saturation level can be used as a measure of the progress of succession. For example, the lower the water depth, the closer the community is to the final stage of succession. The open water and the meadow stages must achieve a reduction in water depth from permanently flooded to temporarily flooded. This is a longer process and involves greater change than in the wooded wetland stage (Larson, Mueller, and MacConnell 1980). Bog wetland studies have demonstrated that hydric mosses and liverworts decrease the amount of open water by forming mats which slowly fill in the bog (Brewer 1988). It seems reasonable to assume that similar growth patterns of bryophytes occur in swamps. Thus, hydric swamp moss and liverwort species probably have the same role as hydric bog species. As the water depth is reduced, more xeric moss and liverwort species become dominant over the hydric species. Thus, the moss and liverwort species can be used as a differentiating factor for communities exhibiting the same successional stage of their vascular vegetation. Analyses that evaluate bryophyte community dynamics can more accurately determine the exact stage of succession.

The QS and multiple similarity show a continuum of the mosses and liverworts from one successional stage to another. Thus, if the pioneer moss and liverwort species aid in the growth of the secondary species (facilitation model) (Clements 1916), the progress of succession will probably be accelerated. The successional progress will probably proceed slower if the secondary species cannot dominate until the earlier species become extinct (initial floristic model) (Egler 1954). Four different successional paths in the study area will be dealt with separately.

Species richness of the vegetation communities to the west of Area F will be examined first. Areas F and E appear to be approximately equivalent communities because each contains only one species, *Amblystegium riparium*. In this case, other variables such as water depth are required to differentiate between these areas.

Another successional community, Area C, has no similarity to Area E; they share no moss or liverwort species. This suggests successional differences in Areas E and C. It appears that *Amblystegium riparium* is a pioneer species for this successional progression. However, cover data show some similarity in the two communities. The pioneer species, *Amblystegium riparium,* is present in Areas E and C. Two secondary species, *Entodon cladorrhizans* (Hedw.) C.M. and *Frullania inflata* appear to be colonizing Area C. Differences in the availability of substrates suitable for colonization by bryophytes is suggested as the probable cause of differences in species richness. The higher similarity ratios indicated that the successional progress from Area C to Area B is high in continuity. New species colonization is likely in progress while the other species are established. For Areas B and A, the similarity was slightly less than for Areas C and B. Therefore, there are fewer species in common for A and B than for C and B. As Area A is nearest the endpoint of succession, a greater number of new species can invade and yet not become dominant species. The moss and liverwort successional progression from Area E to A is representative of Clements' (1916) facilitation model. It appears that the pioneer species, *Amblystegium riparium,* may be reducing its dominance by creating a more suitable habitat for the secondary species, since the two secondary species, *Amblystegium serpens* and *Haplocladium virginianum,* almost equal *A. riparium* in cover in the last stage (Area A).

Looking at the successional progress from east to west indicates the first communities, Areas F and G, had no similarity. This is most likely due to the differences in substrates available for colonization. The successional transfer between Areas G and H also had no continuity. Egler's (1954) initial floristic composition model is represented by this westward successional progress, since it appears that secondary species exist only if the pioneer species are extinct. Again, the result probably reflects a difference in substrates available for colonization. This indicates that there is no continuity between the westward successional communities, even though their vascular vegetation exhibits a successional continuum. This suggests that the dominant mosses and liverworts have a very narrow habitat preference. Liverworts or mosses occurring in one or two habitat types have been demonstrated to have a narrow range of ecological tolerance (Chaffin et al. In Press).

In successional progress moving north or south, no similarity is observed between Area F and Area D. However, the pioneer species, *Amblystegium riparium,* decreased in cover, and three secondary species, *Amblystegium serpens, Anacamptodon sphlachnoides* (Froel. ex Brid.) Brid., and *Entodon compressus* C.M. were dominant. The facilitation model is represented by this moss and liverwort successional progression (Clements 1916), suggesting a response to differences in the vascular vegetation of these communities.

According to Lui (1991), clustering data showed that the vascular vegetation of the eight communities exhibited a similar relationship as represented by the moss and liverwort data. Areas A and B were found to be slightly similar, Areas B and C were higher in similarity, and Areas E and F were most similar. The moss and liverwort no similarity areas were also distantly related according to vascular vegetation data.

The QS and multiple similarity values describe the general successional development of GBWMA. Considering the specific community analyses (equitability and heterogeneity) and the data comparing these specific analyses (linear regression and step-wise linear regression) offers a more direct examination of the successional progress.

Because of the successional progression occurring at GBWMA, a definite pattern is apparent in the heterogeneity and equitability values. The heterogeneity values increase moving along all cardinal points from Area F. As the successional stages progress from Area F, the cover of the most common species increases. However, the data indicates a decrease in cover of the dominant and pioneer species, *Amblystegium riparium,* in every successional direction. This shows that the secondary species are beginning to flourish because of the possible aid of the pioneer species (facilitation model) (Clements 1916). Heterogeneity suggests that the westward successional progress is representative of the facilitation model, but the QS and JC suggest the initial floristic composition model.

Equitability values generally increased with successional progression of vegetation communities. In addition, moss and liverwort cover increased with successional progress. Equitability values suggest that secondary species are colonizing and flourishing. This supports Clements' (1916) facilitation model which states that the last stage of succession will have an even cover of mosses and liverworts.

The following three interactions were studied to determine their effects on one another and the overall successional development: coverage versus heterogeneity, water depth versus heterogeneity, disturbance versus heterogeneity. In the present study, a negative correlation is shown between cover and heterogeneity.

Barkman (1958) reported that the Dutch flora has lost 15 percent of the terrestrial bryophytes because of disturbance. However, some bryophytes benefit and flourish from disturbance (Carvey, Farrar, and Glenn-Lewin 1977). Disturbance values ranging from one to six were used to represent minimal, intermediate, and intensive disturbance. Disturbance values and heterogeneity (Simpson's) were strongly negatively correlated. This suggests that at least some moss and liverwort species colonize where disturbance is minimal. The majority of the communities of this study have intermediate disturbance. Weaks et al. (1991) found that the majority of the Upper Shavers Fork Basin's moss species occur in intermediately disturbed forest habitats. Whittaker's (1970) and Connell's (1978) hypothesis predicts that when disturbance is

intermediate, species diversity will be higher. Weaks et al. (1991) found intensive disturbance will cause a decrease in bryophyte species diversity.

Water depth was strongly negatively correlated to heterogeneity. Area F, which had the highest water depth, also had the lowest species diversity. Chaffin et al. (In Press) reported similar findings in studies of sparsely colonized substrates located within a periodic flood zone. It was suggested that flooding is a major factor affecting liverwort species richness and cover.

Heterogeneity, equitability, species richness, and diversity were compared to evaluate their influence on successional progress. Heterogeneity, equitability, and diversity were established to be equally important factors in successional progress. These values more adequately describe ongoing succession than species richness and should, therefore, be used to identify the precise stage of succession of a vegetation community.

8 Behavioral and Physiological Ecology of Dragonflies (Odonata: Anisoptera)[1]

Introduction

No information was found in the literature on food habits, growth, or development of odonates from freshwater swamps. Studies on territoriality and mate guarding (Jacobs 1966; Waage 1979 a,b), feeding habits (Buskirk 1989, Merrill and Johnson 1984) prey refuge (Benke 1976 and 1978, Johnson et al. 1985), and population structure (Paulson and Jenner 1971) are common from both lotic and lentic environments. This study was prompted by the lack of knowledge of odonates abiding at GBWMA and also the dearth of literature on odonates residing in any freshwater swamp. Additionally, the information will provide baseline data prior to habitat modification by the U.S. Army Corps of Engineers, Huntington District.

The type of habitat at GBWMA is a rarity in mountainous West Virginia. Wetlands account for less than 10 percent of the state's total surface area (Jones 1992). Adult female dragonflies utilize the wetland vegetation (e.g., cattails and sedges) as prime oviposition sites. Additionally, many naiads require weedy areas with adequate food resources for growth and development.

Dragonflies and damselflies comprise the order Odonata. Odonata contains three suborders: (1) Anisoptera, dragonflies with the fore and hind wings different in shape; (2) Zygoptera, damselflies which are small and delicate, with all the wings similar; and (3) Anisozygoptera, which superficially resemble the Anisoptera but are intermediate in several important respects between the two other suborders (Corbet 1962). Odonates exhibit incomplete metamorphosis, having no pupal stage separating the adult from the naiad. The naiad, which bears little resemblance to the adult, is adapted for an aquatic existence. Winged adults mate above water, and the female lays her eggs immediately. During copulation, the male may be attached to her thorax (i.e., "in tandem"). Aquatic and carnivorous, the naiad grows by successive molts (9 to 14) and

[1] Donald C. Tarter, Ph.D.; Lee Ann Mullins, M.S.

subsequent instars. Towards the end of the final instar, the tissues inside the larval cuticle change into those of the adult (Corbet 1962). These internal changes comprise metamorphosis. When metamorphosis is complete, the naiad leaves the water and undergoes a final molt during which time it transforms into the winged adult.

There were four objectives of this investigation:

a. To provide a species list of resident odonate populations within GBWMA prior to habitat modification resulting from the addition of marshlands by building dikes.

b. To determine the magnitude of territoriality in the adult dragonflies.

c. To examine density-dependent cannibalism in naiadal adonates involved in fish exclusion experiments and the impact of fish predation on their abundance and species composition.

d. To determine the food habits for a comparison study between *Erythemis simplicicollis* and *Pachydiplax longipennis*.

Related to the second objective, territorialism has been studied extensively in vertebrates, but invertebrates in general have received little attention. Territorialism is related to sexual selection, and insects, such as dragonflies, whose mating activities are highly localized and overt, are well suited for such studies. Darwin (1871) included dragonflies among the insects to illustrate his concept of sexual selection. Noble (1939) has presented a general definition of a territory as "any defended area," thereby leaving function to be described in relation to a particular case.

This typical mating system of territorial odonates is resource defense polygyny in which males defend oviposition sites and thereby gain access to the receptive females. Among odonates, there is great diversity in the extent to which males guard their mates after copulation. Males may remain in tandem with their mates while they oviposit, or they may perch or hover by them, repelling competitor males from the area near egg-laying mates. A third major alternative is to release the female after mating and subsequently ignore her while she oviposits. Guarding is thought to represent an attempt by the male to prevent his mate from accepting another male. If the female copulates again, she may use her last partner's sperm, resulting in a reduction in egg fertilizations by her original mate. During the time when density of territorial males is greatest, between 1000 and 1200 hr, receptive females often leave their perches to fly out over the water where they are captured by and mated with waiting males (Alcock 1982). Of the 32 observed copulations by territory owners, 30 took place within the male's territory (Alcock 1982). In every instance, the male first flew with the female around his territory. In only 18 of 27 cases did the pair alight on a rock or tree limb in the territory. In the other 9 of the 27 cases, the male abandoned his territory to accompany the female in search of another oviposition site. If a pair were not disturbed at a suitable

location, and if the female stopped or slowed her wing beat, the male alighted quickly and released the female at once, permitting her to slip down to the water to explore the plant matter.

Females benefit from being guarded during oviposition and are not affected by gamete displacement as are males. It is equally advantageous for females to be guarded by mates or nonmates. Females may leave or be chased from their mate's territory before completing oviposition. Gaining access to a new oviposition site by mating with the resident male involves time delays and increased risks of predation. This can be avoided by joining other females already ovipositing with a guarding male. Additional advantages to joining ovipositing females that could outweigh the potential disadvantages of over-utilization of oviposition sites include the following: 1) presence of several females may indicate the male is a successful guarder, 2) it may indicate a high quality oviposition site, and 3) the presence of other females (safety in numbers) may indicate or provide safety from predation from frogs and fish (Waage 1979b).

Sympetrum parvulum

In at least one odonate, there is intraspecific variation in the intensity with which males guard a recent partner. Ueda (1979) found that nonterritorial males of *Sympetrum parvulum* escort their ovipositing females in tandem, but only when the density of males is high. Presumably at these times the risk of losing a mate to a more dominant male is relatively high.

Erythemis simplicicollis

Females of the dragonfly *Erythemis simplicicollis* store enough sperm to fertilize 6 to 13 clutches of eggs laid on consecutive days. Males wait for females at ponds containing surface vegetation on which the females lay eggs. Weather permitting, females usually lay a clutch of eggs every day, and mean clutch is 740 eggs. Some males defend vegetation; others act as satellites. After mating, both types of males attempt to guard females against takeover by other males. During an average copulation of 20 sec, the male would be removing or repositing sperm for the first 15 to 18 sec, and only in the terminal seconds would he insert the contents of his penis vesicle (Waage 1979a). Interruptions could conceivably prevent the male from inserting his own sperm. In summary, most female *Erythemis* carry viable sperm for 4 to 5 days, sufficient to fertilize at least 5 or 6 clutches laid on consecutive days. *Erythemis* replace an average of 64 to 74 percent of the stored sperm of the females (Waage 1979a). A male does not mate several times with the same female because he would only be removing his own sperm again and gaining nothing, while losing time and opportunities. A male will mate again with the same female if she is chased from the pond and returns more than 15 sec later. In this case, the male could not be sure that she was the same individual or that the female had not mated again elsewhere. The possibility of male sperm

competition arises because females mature and oviposit a clutch of eggs daily and can store viable sperm for at least 5 days, some as long as 12 days.

Plathemis lydia

Males of the *Plathemis lydia* species defended certain traditional areas for the primary purpose of mating. Males interact aggressively with each other to establish a dominance hierarchy, and each individual in the area appears to recognize and maintain the territorial boundaries. Thus, territories of *Plathemis* were not used exclusively by a dominant individual. This involved the recognition of dominance and submission by the insects using a particular area, so that the dominant male was most successful in mating attempts. Campanella and Wolf (1974) described the territoriality and mating of *Plathemis* as a temporal lek system, where males return to a traditional communal site for the primary purpose of mating. Within the temporal lek system, the most dominant individuals command the optimum time for reproductive activities. The temporal lek system described for *Plathemis* seems to be a complex evolutionary solution to the problem of high density of males, reproductive individuals competing for the limited resources of space, time, and females.

Immature males fly in a slower, more fluttering manner than older males and may temporarily chase *Anax junius* males as if mistaking them for females of their own species. They quickly seize females of their own species, but sometimes make abortive copulations. They are less active in guarding ovipositing females than are older males and are easily driven from the pond by the latter.

Nonterritorial males attempt matings with females opportunistically encountered on shore or at temporarily unguarded oviposition sites. While their mating expectancy may be the same or lower than territorial males, they devote no time and energy to territorial acquisition and defense or to postcopulatory guarding. Because of sperm displacement, the reproductive success of these males depends upon the ability of their mates to exploit the guarding behavior of territorial males. It is uncertain whether nonterritorial males represent an alternative mating tactic supported by territorial male guarding behavior or whether they are young or older males unable to acquire or keep territories.

Regarding the third objective, Johnson et al. (1985) conducted field enclosure experiments designed to determine the intensity of intraspecific and interspecific competition at approximately natural densities. Survival rate for both species was dependent on intraspecific density. These effects are attributed to interference (encounter) competition rather than to exploitation (consumption) competition. The mechanism of competition seems to be predation by larger naiads on smaller naiads. Morin (1984a) conducted a similar experiment designed for variance analysis to measure the impact of fish and early-breeding odonates on the abundance and species composition of late-breeding odonates. Fish exclusion increased the combined abundances of all anisopteran species

5 to 10 times above abundances in pens containing fish. Early breeders did not reduce late breeder recruitment in pens with fish. Different histories of colonization by early breeders influenced interspecific interactions among odonates only if fish were absent. Tested was the hypothesis that two damselfly species differ in vulnerability to predation with laboratory feeding trials using two abundant vertebrate predators, adult red-spotted newts and juvenile bluegills (Pierce, Crowley, and Johnson 1985). For each foraging trial, 10 naiads (five of each species) were placed in an aquarium for 18 to 24 hr before introducing a predator. The data were analyzed using the binomial test. Results illustrated that one species was more vulnerable to predation than the other. This paper by Pierce, Crowley, and Johnson (1985) prompted the present study in which two competitive species of dragonflies were tested using bluegill (*Lepomis macrochirus*) as the predator.

Related to the fourth objective, dragonfly naiads are generalized carnivores, feeding on any aquatic animal of an appropriate size that they can capture. Feeding behavior has been described by Merritt and Cummins (1984) as following three phases: (1) detecting prey and adjusting position in relation to it; (2) ejecting the labium to grasp the prey; and (3) employing the mandibles to devour the prey. When an organism is sighted, the immense labium, resembling a large prehensile arm, extends quickly to grasp prey then is drawn back again very swiftly. The sharp hooks and spines of the palpal lobes clutch the prey, and the jaws cut it into pieces for ingestion. Any fragments remaining are caught in the prementum and also consumed. This efficient mechanism requires enough room to reach out for prey and is occasionally subject to entanglement in threads of filamentous algae and other slender, multicellular plants (Merritt and Cummins 1984).

Taxonomy, Distribution, and Habitat

Taxonomy

Kingdom Animalia
- Phylum Arthropoda
  - Class Insecta
  - Subclass Pterygota
  - Infraclass Paleoptera
    - Order Odonata
    - Suborder Anisoptera
      - Family Libellulidae Selys
      - Subfamily Libellulinae Selys

Genus *Erythemis* Hagen 1861. Syn.: *Mesothemis hagen.* The naiads of this genus are readily identified by the strongly decurved parapcrocts and cerci. The labium is armed with long premental and lateral setae and numerous spinules along the smooth distal edge of the palpa. The large compound eyes laterally located on the head are green or yellow-striped when alive. The

abdomen is short and stubby and green to brownish in color. It bears no dorsal abdominal hooks or lateral abdominal spines (Olson 1972).

Erythemis simplicicollis **Say 1839.** The coloration of this naiadal species is quite variable. Although several specimens taken had a red coloration on the ventral surface, this is the only species common to this area (Olson 1972) (Figure 20).

Genus *Pachydiplax* Brauer 1868. The naiad is smooth and depressed of body with a wide head. It is generally dark in color, with transverse banding of the femora (Needham and Westfall 1955). The abdomen has no dorsal hooks but has lateral spines on segments 8 and 9 (Olson 1972).

Pachydiplax longipennis **Burmeister 1839.** This is the only species known in the genus *Pachydiplax* (Olson 1972) (Figure 20).

Distribution

Erythemis simplicicollis. Distribution and dates. Canada: Ont., Que.; United States: AL, AZ, CA, CT, FL, GA, IL, IN, IA, KS, KY, LA, ME, MD, MA, MI, MN, MO, MT, NB NV, NG, NJ, NY, NC, OH, OK, OR, PA, RI, SC, TN, TX, UT, VA, WA, WI, WV; Mexico: Baja Calif., Tamaulipas; Antilles: Cuba, Haiti, Jamiaca.

Year-round southward (Needham and Westfall 1955). West Virginia Counties: Cabell, Gilmer, Greenbrier, Lincoln, Mason, Pendleton, Pocahontas, Summers (Olson 1972) (Figure 21).

Pachdiplax longipennis. Distribution and dates. Canada. B. C., Man., Ont.; United States: AL, AZ, AR, CA, CT, FL, GA, IL, IN, IA, KS, KY, LA, ME, MD, MA, MI, MN, MS, MO, MT, NE, NV, NJ, NY, NC, OH, OK, PA, RI, SC, TN, TX, UT, VA, WA, WV, WI; Mexico: Baja Calif., Coahuila; also from the Bermudas and Bahamas.

Collected every month in Florida (Needham and Westfall 1955). West Virginia Counties: Cabell, Dodridge, Gilmer, Greenbrier, Mason, Putnam, Wayne, Wood (Olson 1972) (Figure 21).

Habitat

Both species of odonates are sprawlers. They are the most abundant dragonfly among the silt and vegetation of the 60 ha of lentic waters in GBWMA.

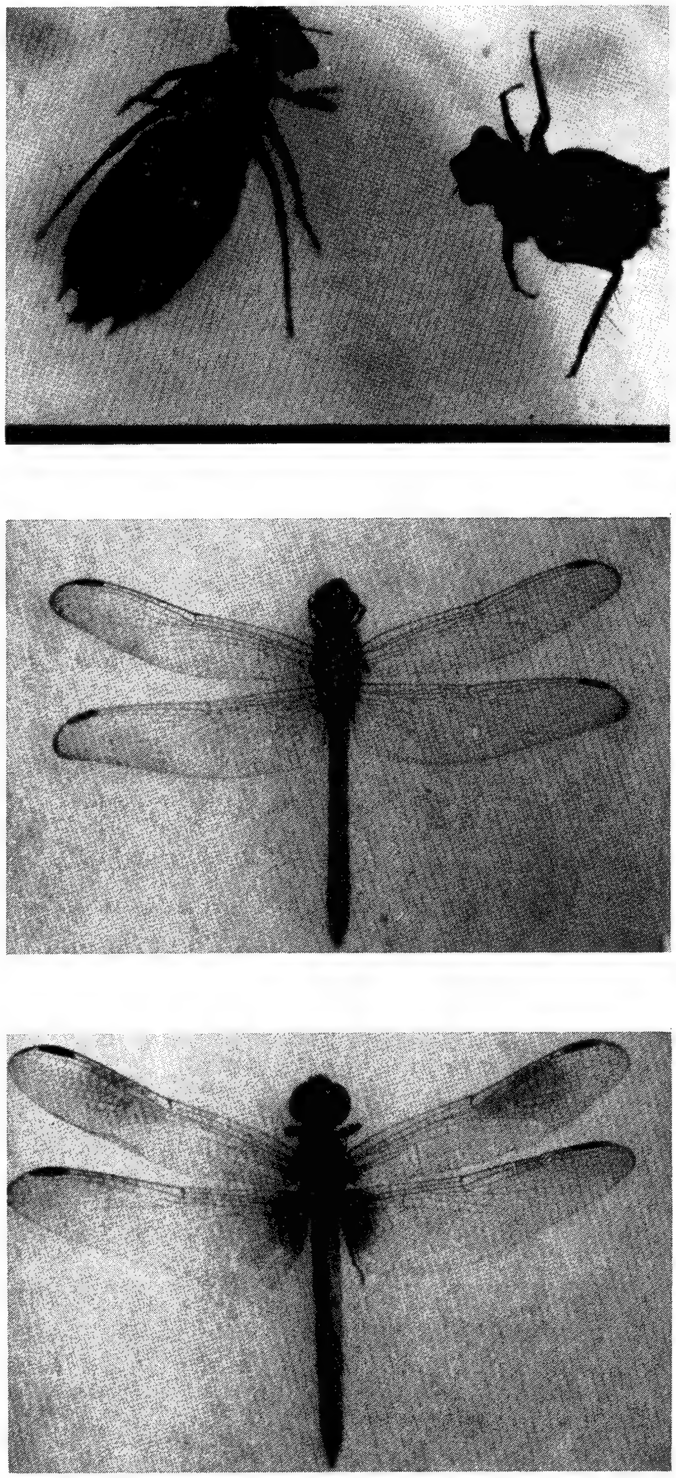


Figure 20. Photographs of *Erythemis simplicicollis* and *Pachydiplax longipennis* in the naiadal and adult stages of life

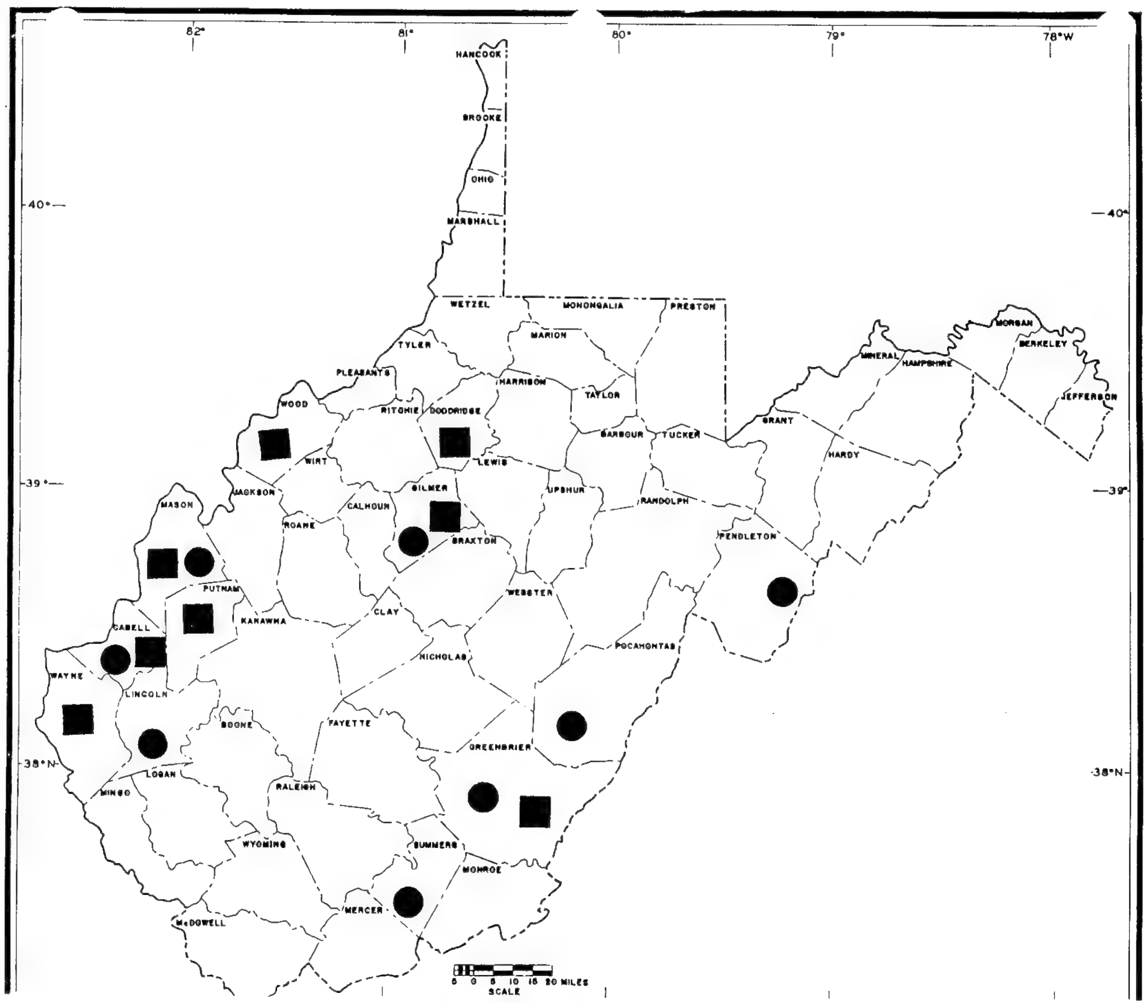


Figure 21. Distribution map of counties in West Virginia containing *Erythemis simplicicollis* and *Pachydiplax longipennis*
Note: ■ represents countries containing *Pachydiplax longipennis*, ● represents countries containing *Erythemis simplicicollis*

Methods and Materials

Field studies

Benthic sampling. Naiadal dragonflies were collected from the 0.4 ha wooded swamp with a fine mesh (60 threads/in.) hand dredge by taking 3 m^2 of substrate, vegetation, and surface mud from the study area at the end of each month. A 1-m^2 grid of PVC pipe was used to delineate the collecting area (Figure 22). The substrate was sorted in the field, and the naidal odonates removed and preserved in vials were returned to the lab and searched for small instars. Weather permitting, these procedures were repeated monthly from October 1992 through October 1993.

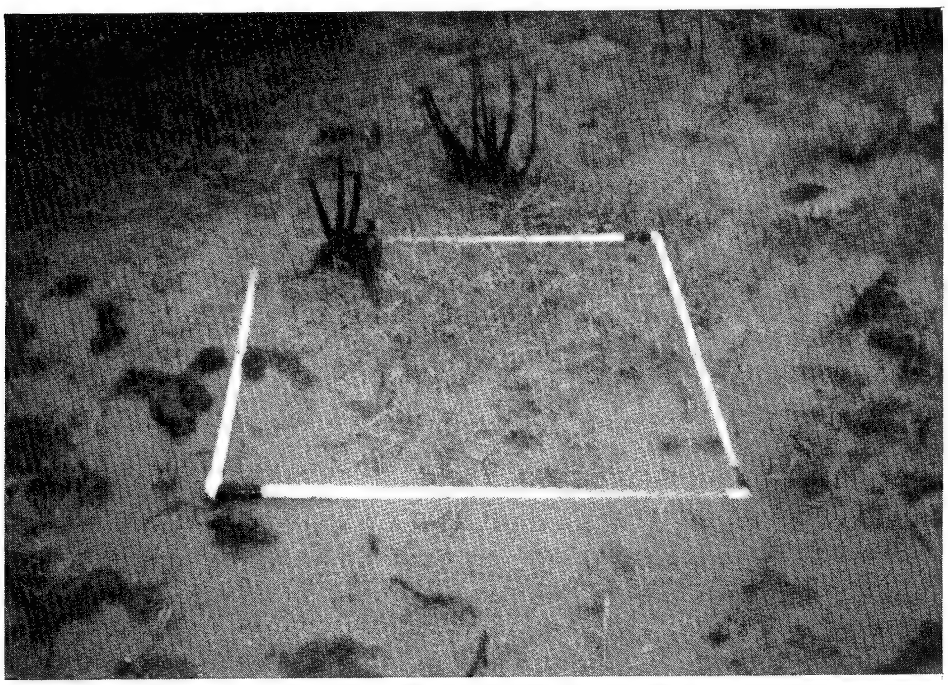


Figure 22. Square meter kick sampler used for benthic collections at GBWMA

Water quality and temperature. During each monthly collection, temperature (°C) and water quality were assessed using a Hach kit. Tests included dissolved oxygen (mg/L), alkalinity (mg/L $CaCo_3$), CO_2 (mg/L), total hardness (mg/L $CaCO_3$), and total acidity (mg/L), and pH. A maximum-minimum thermometer was kept and the water quality tests performed in the same location to ensure continuity.

Collection of adults. Adults were captured using butterfly nets and carefully placed in killing jars containing cyanide. They were taken back to the laboratory and mounted for identification. During the summer months of 1993, an observational experiment was performed in which adult dragonflies were tagged and observed to study territorial behavior, mate guarding and acquisition, and ovipositing. Flight periods of all odonates abiding at

GBWMA were charted. Night trips provided times of emergence and positive identification of a naiad with a winged adult.

Territoriality. The perimeter of Tom's pond was gridded at 6-m intervals, 0.5 m from the edge, to facilitate recording the locations of individual dragonflies and/or their prospective territories. On 10 August 1993, dragonflies of the species *Plathemis lydia, pachydiplax longipennis,* and *Erythemis simplicicollis* were marked with small dots of enamel paint on the wings and on the dorsal surface of the abdomen; a total of 29 males and 4 females were marked. Total body length (eyes to claspers) of captured individuals was measured using calipers, and the condition of their wings was noted as fresh (shiny with no nicks or breaks); medium (not shiny but with only minor nicks); or worn (whitish, often with major breaks). Observations consisted of female (mating) census; male census, and focal male watches.

Female census was conducted on 11 August 1993, from a rubber raft stationed in the center of the pond. This vantage point allowed a view of the entire pond. Time of arrival and location of copulation and oviposition of females arriving on the pond during continuous 30-min watches were conducted once each hour throughout the day.

Male census was conducted simultaneously on 11 August 1993, from the same vantage point. Census was done at hourly intervals recording the activity, location, and identity of all marked males as well as noting the number of unmarked males present. Each marked male was watched 1 to 2 min during the census. Males who patrolled a localized area and actively excluded other males from this area were considered to be territorial (Noble 1939). Males that were not patrolling the pond edge were not localized in their movements; those that failed to defend the area in which they were located against intruders were considered to be nonterritorial. Territory size was determined by the extent of patrol flight and chases of intruding individuals. Estimated daily mating success (EMS) of males was determined based on the temporal and spatial distribution of female ovipositions. Each time a male was observed to be territorial during one of the hourly censuses, his mating success during that hour was estimated as the proportion of ovipositions observed during the female censuses to have occurred within the confines of this territory, multiplied by the average number of ovipositions occurring during the hour that he was recorded. To arrive at a total daily EMS, estimates were summed for each hour of the day that an individual was observed to be territorial.

Focal male watches involved continuous observation of the reproductive behavior of an arbitrarily chosen male. Whether or not the male was territorial during the watch was determined by the criteria discussed above. The number of copulations obtained by the focal males, the number of times their mates successfully oviposited, and the number of oviposition dips by these females was recorded. In addition, the males' locations on the pond, activities, and the number of conspecific males within 1 m of the focal males were recorded. Activities included perching, flying, mateguarding, and intraspecific male-male chases.

Laboratory studies

Predation experiment. Naiads were collected from GBWMA using fine mesh hand dredges (60 threads/in.). They were acclimated in 10-gal aquaria with natural detritus and observed for an adjustment period of 17 to 23 hr. Odonates were separated and categorized by size and species.

Naiads were maintained at room temperature (19 to 22 °C) with natural intensities and durations of light and dark. Bluegill were a mixed collection from GBWMA and a small farm pond in Wayne County. They were maintained at room temperature, exposed to natural intensities and durations of light and dark, and fed a variety of items several times per week.

Experiments were conducted in 10-gal aquaria containing filtered swamp water and a substrate of detritus previously autoclaved to remove all macroinvertebrates.

For each foraging trial, 10 naiads (five of each species) were placed in an aquarium 18 to 24 hr before introducing a predator. Within-trial naiadal size was standardized by randomly selecting five of each species from a group of similar sizes. Four bluegills (107.4, 106.9, 101.5, and 125.4 mm) were used as predators. In each foraging trial, a solitary predator foraged for 12 hr. A 12-hr foraging period for bluegills was sufficiently long that enough naiads were eaten by each predator to resolve differences in vulnerability. This time was short enough to prevent switching from one species to the other as the more vulnerable species became depleted. The predator was removed after 12 hr and the substrate thoroughly sorted to recover surviving naiads. One replicate trial (48 hr between trials) was run. Predator-free trials controlled for either intraodonate predation or incomplete retrieval of naiads. Data (numbers eaten) were analyzed with the binomial test, which tested the hypothesis that one species is more vulnerable to predation than the other. Data were further analyzed using the Fisher Exact Probability Test.

Head width measurements. For growth determinations, measurements including head width (mm), total length (mm), and wing pad length (mm) were taken using calipers. Population range diagrams showed range, mean, standard deviation, and standard error of the mean for each season. Growth rates were calculated for each season.

Foregut and scat analyses. A majority of all *Erythemis simplicicollis* and *Pachydiplax longipennis* naiads from the monthly collections were used for foregut analysis. Microdissection scissors were used to remove the head and to make a ventral mid-thoracic cut in the naiad. The foregut was removed from the thorax using microdissection tweezers and placed in a 1-ml centrifuge tube containing 70 percent ethanol. After all of the foregut was removed, the identities of the food items were determined to the lowest possible taxon according to Merritt and Cummins (1984). The volume that each food item occupied was estimated according to a point method devised by Hynes (1950), where each foregut is allotted a specific number of points based on its fullness

(distended, 30; full, 20; three quarters full, 15; half full, 10; one-quarter full, 5; trace, 2; empty, 0).

The points received by each type of food item were used to calculate percent total volume = total number of points per given food item/total points awarded per study period. Diet overlap values were determined for seasons using the indices of Horn (1966) and Morisita (1959). Using the Horn (1966) and Morisita (1959) indices, the percent similarity of overlap in the diets was calculated. Calculations were used to compare this data with food studies in the literature.

Gut analyses were compared with fresh fecal remains of live naiads that were kept in sectioned petri dishes filled with distilled water. Naiads were not fed during the three days in which they were monitored.

Rearing and growth. On 13 July 1993, an ovipositing female *Pachydiplax longipennis* was captured. Held by her forewings, her abdomen repeatedly dipped in a jar containing water, she continued to lay eggs. The eggs were then returned to the laboratory and placed in a 10-gal aquarium filled with distilled water that was maintained at the present temperature of the swamp (23 °C). The eggs hatched after 2 weeks. Naiads were monitored closely and were examined daily by the use of a magnifying light. Three separate instars were preserved (each instar lasted approximately 10 to 14 days) before a fungal infection killed the remaining naiads.

Respiration. Oxygen consumption of *Erythemis simplicicollis* naiads at two temperatures was measured using a Gilson differential respirometer. Twenty naiads were collected from GBWMA, transported to the laboratory, and allowed to equilibrate for 24 hr. Eight naiads along with a small amount of swamp water were placed in separate reaction flasks. Three milliliters of potassium hydroxide (KOH) (10 percent) were placed in the center wells of the reaction flasks. A piece of filter paper served as a wick to increase the surface area for the KOH to absorb any carbon dioxide produced by the dragonflies. Anhydrous lanolin was applied to the top of the center wells to prevent seepage of the KOH. Also, the glass joints between the respirometer and the reaction flasks were lubricated with lanolin to create an air-tight system. Eight reaction flasks attached to independent manometers were lowered into the water bath equilibrated to 19 °C (room temperature). Naiads were allowed to acclimate for 2 hr in the reaction flasks. Twelve hourly readings were taken with the temperature maintained at 19 °C. Following the last reading, the temperature was lowered to 11 °C, a representation of fall/spring. Naiads were allowed to acclimate overnight at 11 °C before the 12 hourly readings were taken at this temperature. These data were used to compute an hourly average oxygen consumption for the dragonflies. The average hourly consumption value was divided by the weight of the naiad to provide microliters of oxygen per milligram body weight. A regression analysis was used to determine whether a relationship existed between body weight and oxygen consumption. The mean and standard deviation were computed from each set of data, and a t-test (<0.05 confidence level) was used to determine any significant

differences. At the conclusion of the experiment, naiads were removed from the flasks and sacrificed in boiling water. They were allowed to oven dry for 48 hr at a temperature of 94 °C. Naiads were weighed individually using a Sartorius analytical scale, Model 1702.

Low pH tolerance (LD_{50}). Sixty naiads were collected from GBWMA using fine mesh hand dredges (60 threads/in.). Specimens were sorted and allowed to acclimate for 48 hr. Six *Pachydiplax longipennis* naiads were placed in each of the eight watch glasses and exposed to four pH values (1.5, 3.0, 5.0, and 7.0). The pH of each dish was adjusted hourly using sulfuric acid (14 N) until midnight, then checked again the following morning. The pH values were in duplicate and were run for 96 hr, denoting an acute static bioassay. Survivors were allowed to continue for 52 hr more (7 days total) for a short-term chronic static bioassay. After 96 hr, the median tolerance limit (TLm) was calculated using the straight-line graphical interpolation method and the linear regression analysis. After the TLm pH was determined, six *Pachydiplax* naiads were tested at this theoretical pH for 96 hr.

Results and Discussion

Field studies

Benthic sampling. From October 1992 through October 1993, 117 *Erythemis simplicicollis* and 60 *Pachydiplax longipennis* naiads were collected from the wooded swamp site at GBWMA. Relative abundance was based on the number collected per square meter (Figure 23). Naiads were most abundant in the fall and spring and least abundant in the summer during emergence. Naiads were collected exclusively from the wooded swamp because it contained the richest populations of these two species.

Water quality and temperature. Monthly water quality data are shown in Table 1. Total acidity was zero for the entire year and therefore was not included in Table 50. A mean pH of 7.1 suggests that GBWMA is slightly alkaline. Dissolved oxygen ranged from 2 mg/L in July to 6 mg/L in January with a mean of 4.1 mg/L. Monthly water temperature varied from 0 °C in January to a constant temperature of 27.8 °C for June, July, and August (Table 50). Thick ice covered the swamp for portions of January and February; therefore, no water quality data exists for February. The mean annual water temperature was 15.6 °C; the mean air temperature was 14.2 °C (Figure 24).

Emergence and collection of adults. The emergence of naiads was recorded on nightly visits to the swamp. Naiads start to emerge from the water as early as 2100 hr. However, the period from 1100 to 1300 hr seems to be the most opportune time, possibly because there is less chance of predation of the naiad. Naiads crawl up vegetation away from the water approximately 10 to 21 cm, (the distance seems to be species specific). Their

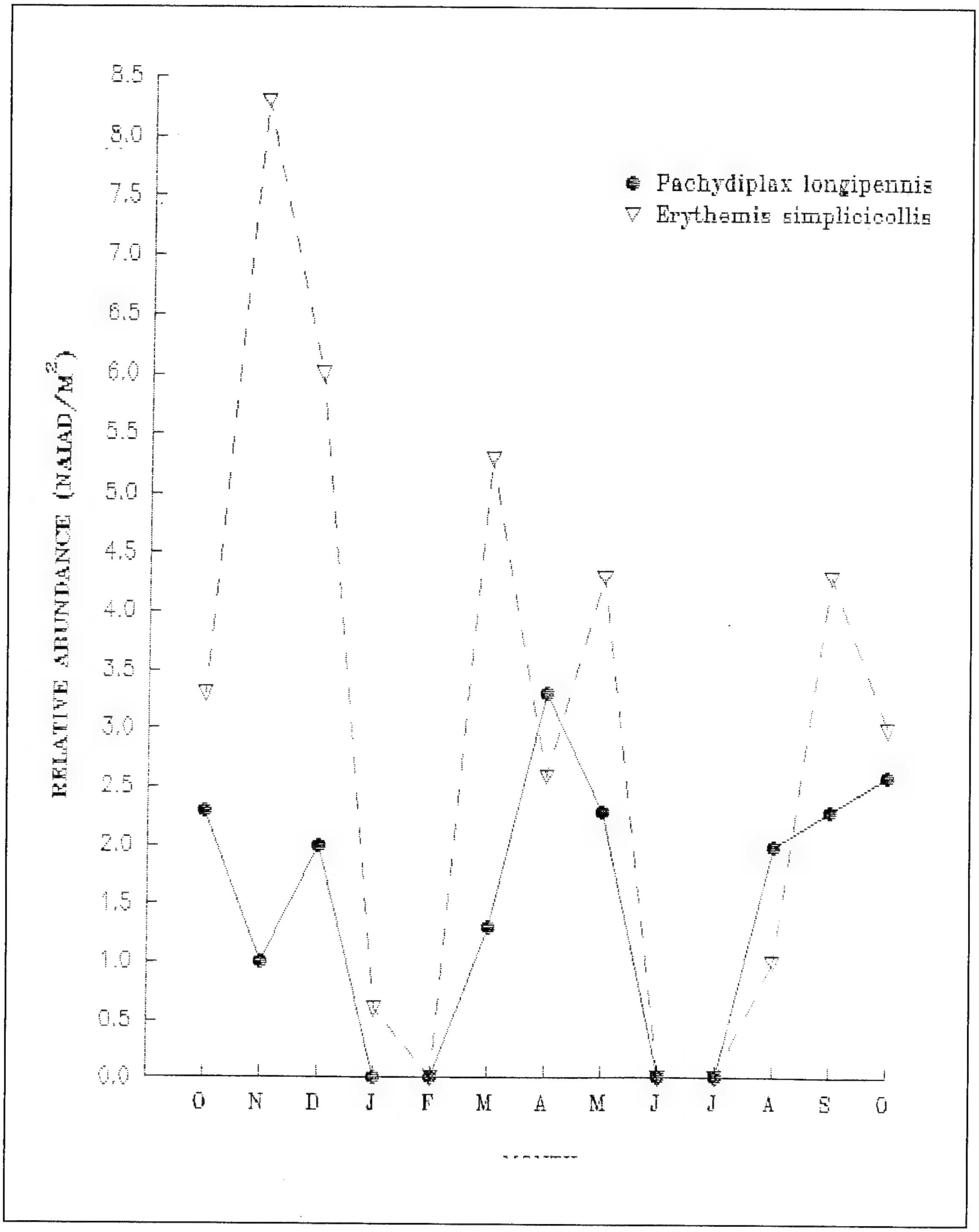


Figure 23. Relative abundance of *Erythemis simplicicollis* and *Pachydiplax longipennis* from monthly collections composed of three 1-m^2 samples

Table 50
Water Quality Data for GBWMA

Dates	Temp, °C	DO	CO_2	ALK.	Hard.	pH
October 1992	8.7	5	10	68	85	6.6
November 1992	7.2	5	10	68	85	6.7
December 1992	8.3	5	10	68	102	7
January 1993	0	6	20	102	119	8
February 1993	[1]	[1]	[1]	[1]	[1]	[1]
March 1993	13.3	4	20	119	119	7.6
April 1993	17.8	4	20	119	123	7.2
May 1993	22.2	4	25	140	102	6.7
June 1993	27.8	3	25	85	102	7
July 1993	27.8	2	15	51	119	6.7
August 1993	27.8	3	20	85	119	7.5
September 1993	16.7	4	20	68	102	7
October 1993	10	5	10	68	102	6.5

Note: All values expressed in mg/L except pH and temperature (°C).
[1] Not collected due to ice.

exoskeletons splits along their backs setting the wings free. Adults immediately begin the long and critical process for drying their delicate wings. The transformation is complete in 8 to 10 hr. Transforming adults were brought back to the lab where they were allowed to complete their transformation. If the adults were given enough room for their wings to dry and expand, they were ready for flight the next morning. But if the jar was too small, or if their wings came in contact with something before they were dry, adults were unable to fly.

In some instances, adults crawled up vegetation that could not support them, and they drowned while drying their wings. Others seemed to lose their grasp or tried to fly when exposed to the light of a flashlight.

Flight periods of all dragonflies abiding at GBWMA were recorded beginning 28 April 1993, with the appearances of the first dragonfly, *Anax junius* (Table 51). *Anax* also had the longest flight period of any of the dragonflies (168 days), 28 April until 13 October (Table 51). *Plathemis lydia*, a libellulid, was second with a flight period lasting 145 days (6 May through 27 October). *Plathemis* was also the last dragonfly recorded for the season. *Sympetrum vicinum*, a fall breeder, did not appear until 30 September and was last sighted 13 October. *Sympetrum* is a migratory dragonfly, so there is reason to believe

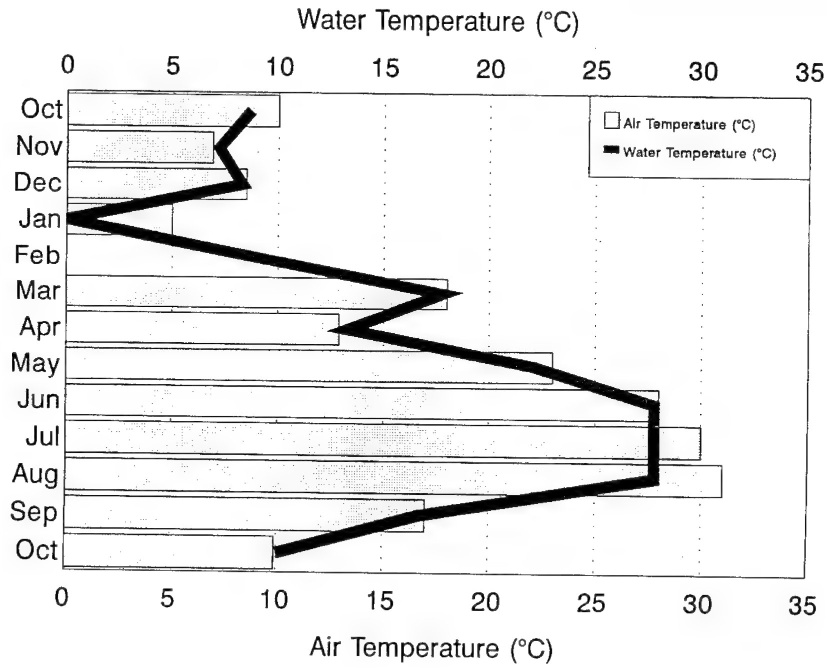


Figure 24. Monthly air and water temperature (°C) from GBWMA

Table 51
Flight Periods of Resident Odonates Abiding at GBWMA During Summer 1993

Species	April	May	June	September	October
Anax junius	28				13
Plathemis lydia		3			27
Pachydiplax longipennis		6		30	
Erythemis simplicicollis		15			8
Libellula cyanea		25		15	
L. puchella		25		15	
Tramea lacerata			8		13
Libellula luctuosa			22	15	
Sympetrum vicinum				30	13

that its breeding season is longer and that contact with the population was lost. Olson (1972) listed *Sympetrum* as one of the most uncommon larval species in Cabell County. *Erythemis simplicicollis* and *Pachydiplax longipennis* are the most abundant dragon flies within the swamp. Their flight periods overlapped considerably. *Pachydiplax* emerged on 6 May and flew until 30 September (Table 51). *Erythemis* was not far behind, emerging on 15 May until

8 October (Table 51). Emergence was correlated with water temperature (Figure 25). No other dragonflies were recorded beyond the last sighting of *Plathemis lydia* on 27 October, on which the water temperature was 12 °C (Figure 25).

Territoriality. Ten of the 33 individuals marked returned to the pond the next day. This number may seem low, but given the thunderstorm that occurred the night after they were marked, the turnout was high. Males began arriving and setting up territories at the pond about 1000 hr, with a few making fly bys as early as 0910 hr. The males secured territories along the shallow side of the pond between posts 4 through 8 (Figure 26). Dragonflies took advantage of the posts which became prime perches throughout the day. No territories were defended along the deeper sections or middle of the pond. This could possibly be the result of fish predation in the deeper water or because males defending favored areas have enhanced mating opportunities. The cost of defending such areas is higher because of increased intruder pressure. However, predation may be important in influencing the spatial pattern of male territorial behavior as well. Species observed eating *Plathemis lydia* were the large aeshnid dragonfly (*Anax junius*) and bluegill (*Lepomis macrochirus*). Thus, it is possible that fish or larger predatory dragonflies were influencing the distribution of males, who may have been putting themselves at risk by defending these favored areas.

Nineteen oviposition events were recorded during the 10 hr of observation. Only nine were from marked individuals (Table 52). The other 10 were recorded from new or unmarked individuals. Ovipositions were not uniformly distributed around the pond. Females avoided the deepest sections of the pond, while 80 percent of the ovipositions took place in a shallow, highly vegetated corner of the swamp between posts 4 through 8 (Figure 26). Males were territorial an average of 0.5 to 1.25 hr (maximum 2 hr). The average territory was 9 m by 6 m (equal to almost the distance between 3 posts). Males patrolled along the pond edges instead of across the pond. The only male observed tolerating subordinates flying within his territorial boundaries was the orange-painted male. He was chased twice from the pond and was afterwards ignored as he passed through the heavily dominated shallow side. This could be because other males did not consider him a threat. The orange male flew in an almost submissive manner, slow and seeming to barely make it from marker to marker. The orange male finally resorted to setting up a territory and patrolling the unguarded deeper side of the pond, but as no females were apparent on that side of the pond, he never secured a copulation.

Territories were always defended solitarily. However, turnover of individuals at specific sites on the pond was considerable, and up to three males defended the same site that day. No satellite or nonterritorial males were observed securing a copulation. So why then are males ever nonterritorial while at the pond? Evidence suggests that there are constraints on the length of time an individual can be territorial. First, males invariably spend only a few hours being territorial on any given day. Second, territorial holders spend

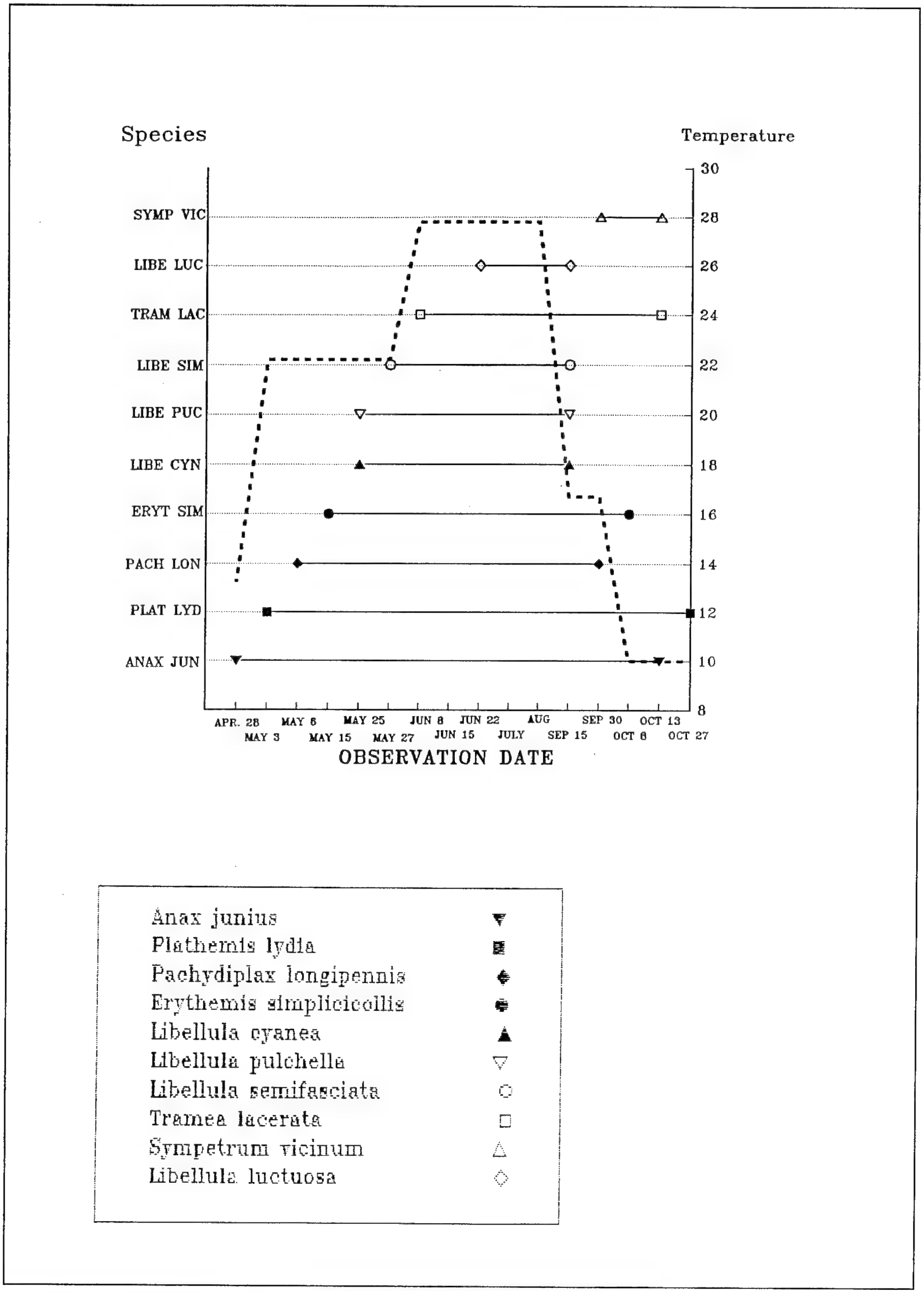


Figure 25. Monthly water temperatures (°C) and flight periods of adults odonates from GBWMA

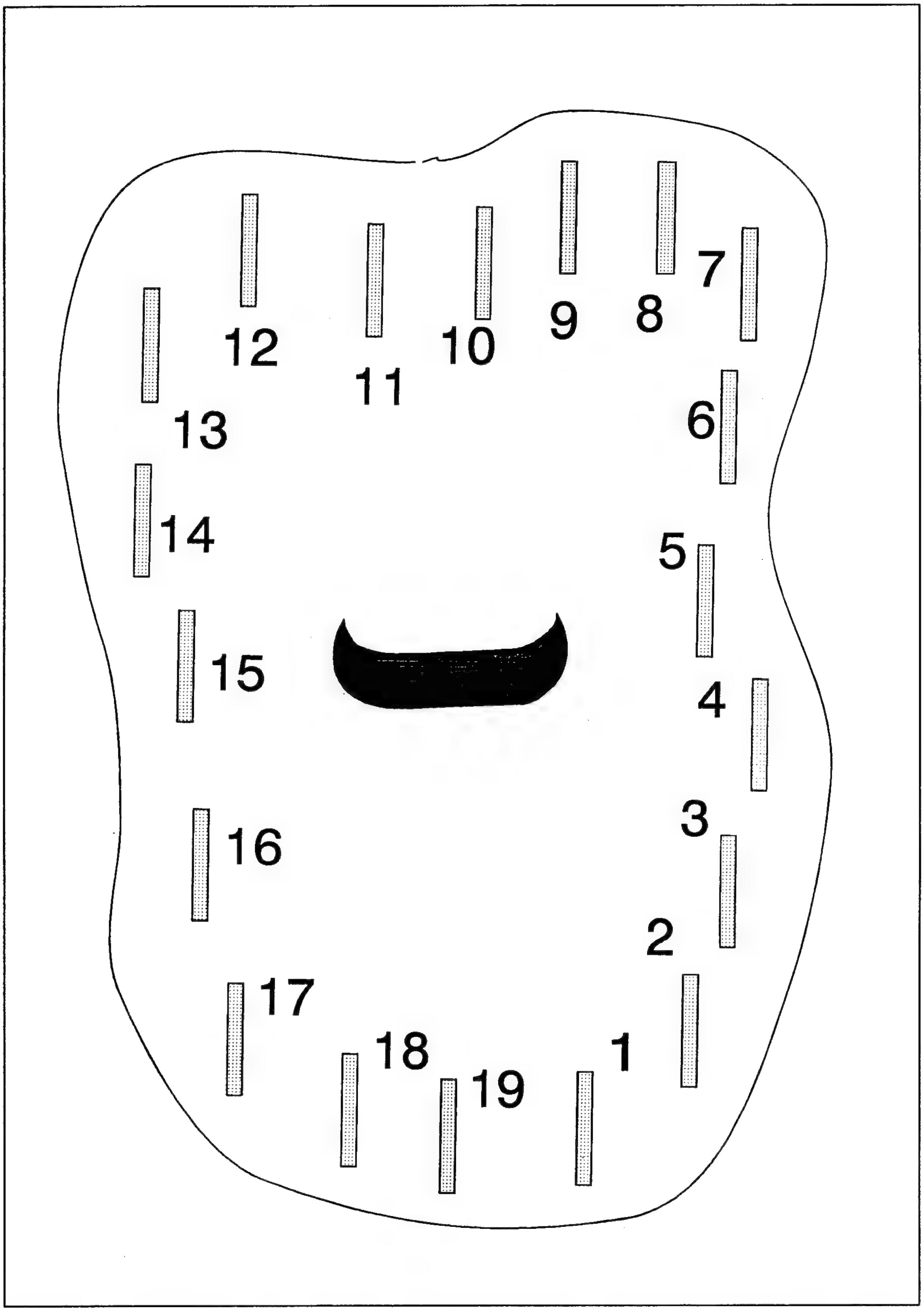


Figure 26. Drawing of Tom's Pond and position of posts from the territorial experiment during summer 1993

Table 52
Marked *Plathemis lydia* Males During the Two-Day Territoriality Experiment at GBWMA

Color Pattern of Marked Males	Activity	Wing Condition	Body Length cm	Time of Day
Yellow	T	1	4.4	1100/1300
Green	T	2	4.7	1300
Orange	T	3	4.7	1400
Orange-Green	T	3	4.5	1300
Brown Red	T	2	4.5	1100
Green-Brown	T	2	4.5	1000
Orange-Yellow	T	1	4.5	1200
Dark Green	T	1	4.5	1100

a high proportion of time in energetically expensive flight (the high activity apparently required in order to retain a territory may be an important factor constraining the duration of territory tenure). That *Pachydiplax longipennis* may operate on an extremely tight energy budget has been demonstrated by Fried and May (1983) who showed that daily food intake barely exceeds the energy necessary to defend a territory.

To determine factors influencing male mating success, daily EMS was correlated with body size and wing wear. EMS was significantly correlated with body size and inversely correlated with wing wear (Table 53). These correlations are apparently due to the tendency for larger males to be territorial longer and to have territories at times of the day when more females are ovipositing (Koenig and Albano 1985).

Ovipositing peaked in early afternoon (1100 to 1300 hr) when male frequency and female occurrence were the highest (Figure 27). The last ovipositing female observed at the water occurred at 1636 hr with the males patrolling the water until 1740 hr. Even though there were still several hours of daylight left, the pond had become shaded, sending the dragonflies off in search of food before nightfall.

Many hours of observation at GBWMA consisted of recording the very complex reproductive behaviors of the dragonflies while defending a territory or a receptive female.

Ovipositing and sperm precedence. A female might submerge and remerge or dip her abdomen at as many as five different locations within and outside her mate's territory during an egg-laying session. If one site does not provide enough ovipositing substrate or refuge, a female will embark in search

Table 53
Wing Condition, Body Length, and Daily EMS of Marked *Plathemis lydia* males

Color Pattern of Marked Males	Ovipositions Within Territory	Average No. of Ovipositions	Daily EMS
Yellow	2/2 1/1	4+5	9
Green	2/3	5	3.3
Orange	0/0	2	0
Orange-Green	0/0	5	0
Brown Red	1/1	4	4
Green-Brown	0/0	2	0
Orange-Yellow	2/4	6	3
Dark Green	1/1	4	4

of another location. If the female flew up from the water, the guarding male recaptured the female but did not copulate again. Instead, the tandem pair promptly resumed the search for another oviposition site. The clutch may be laid on the single day, but sometimes a 2-day period was necessary, after which an interval of 4 to 6 days passed before the female had a new mature clutch of eggs to lay. Travel elsewhere might also benefit the female by enabling her to disperse eggs more widely, thereby reducing the risk that unpredictable fluctuation in water flow, temperature, or pH would result in the destruction of an entire clutch. Ovipositing females may mate more than once during the time they are laying eggs. Males use their penis to remove all or almost all of any sperm stored in the female before transferring their own gametes; as a result, there is a strong last-male advantage. When two or more males mate with a female before she oviposits, their sperms do not necessarily have equal chances to fertilize her eggs. Experiments have revealed a precedence of the sperm from the last male to mate, but lack of precedence and mixing of sperm from successive matings also occurs. In some species, previous sperm may be forced to the rear of the female's sperm storage organs, resulting in a last in, first out phenomenon (Waage 1979a).

Mating, guarding and acquisition. When a male and female left his territory, they were sometimes attacked by owners of the territories through which they passed. If a female oviposited within a male's territory, he generally remained close to the spot where she had been released but would not also repel intruders. After each chase, the male returned to perch near the release point for some time and was almost always in position to recapture the female should she attempt to fly. In contrast, territorial males that accompanied their mates outside their territories behaved in an inconspicuous manner while perched at a release point. They ignored passing males and made no effort to defend the area about the perch unless detected and driven up by a resident male in whose territory they had released the female.

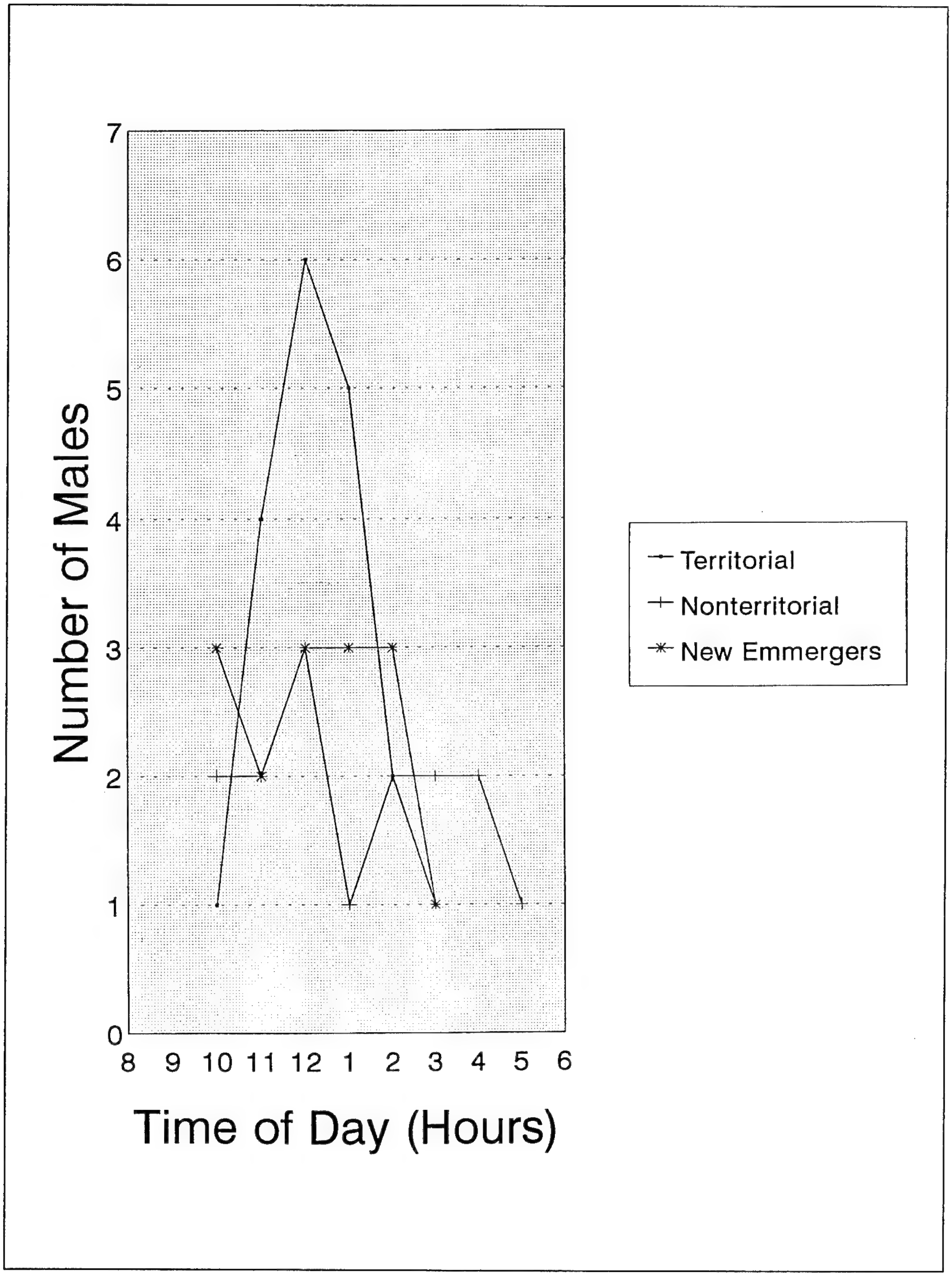


Figure 27. Time and number of hours males of the *Plathemis lydia* species were territorial and nonterritorial during a 2-day experiment in summer 1993 at GBWMA

Nonterritorial and satellite males. The frequency of aggressive interactions was highest during the middle of the day, the time when male density was greatest and when receptive females were most abundant. Individuals made occasional spontaneous flights within their territories and promptly pursued any conspecific male that entered their holdings. Often the intruding male passed directly out of a male's territory, in which case the defender returned to his perch within a matter of seconds. Sometimes the intruder attempted to remain within the territory; a circle flight then ensued. In this interaction the two males chased each other in a tight circle for a variable period of time before one male broke away in a weaving flight that took him out of the contested area. Commonly, in repelling an invader, the territorial resident flew into the territory of a neighbor. This generally led to brief circle flight between the two males with the intruder quickly returning to his own perch site. Thus males were able to defend their territories relatively economically, as most disputes were resolved quickly in favor of the resident. Turnovers in the ownership of territories were probably caused by mortality, voluntary abandonment, and forcible takeover (Alcock 1982).

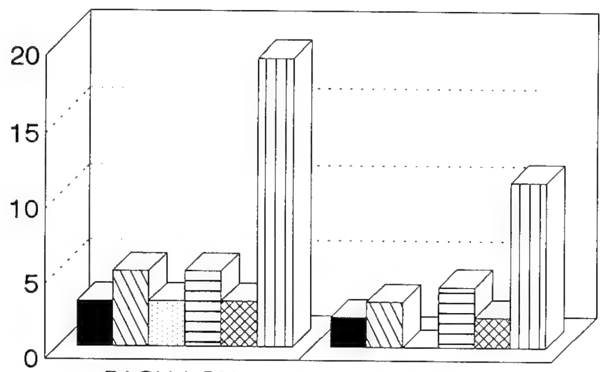
Territorial males secured far more copulations than satellites. Unlike other nonterritoral males (which perched above the water and fed), satellites attempted to acquire mates through the passive occupation of a perch in another male's territory. The role of satellite therefore appears to be a relatively unproductive option that is adopted by young males not yet ready to compete for territory ownership and by older dragonflies after they have lost a territory (Alcock 1982).

Territorial males never employ contact guarding but instead fly near their recent mates. These males should encounter additional receptive females at a higher frequency than the wandering males which are excluded from prime oviposition habitat. The dominant male is free to capture and mate with new arrivals if they become available. However, territory owners may be better able to defend their territories if they are not in tandem.

Laboratory studies

Predation experiment. Sixty-three percent of the *Pachydiplax longipennis* naiads survived compared to the 37 percent of *Erythemis simplicicollis* naiads (Figure 28). *Erythemis simplicicollis* naiads were more vulnerable to bluegill predation than *Pachydiplax longipennis* (Figure 28). In all 5 trials, bluegill ate significantly more *Erythemis* than *Pachydiplax* during laboratory feeding trials (Figure 28). Overall, bluegills ate two times as many *Erythemis* as they did *Pachydiplax* (Figure 29).

Results from the experiment proved to be significant ($p = 0.0934$) (0.05 CL) in that only 11 *Erythemis* would survive occurring 91 percent of the time. The binomial test does not take into account the changing proportion of the population. For example, when one naiad of a species is eaten, the probability of that species being chosen again is lowered, and the other species has a



	PACH LON	ERYT SIM
TRIAL 1	3	2
TRIAL 2	5	3
TRIAL 3	3	0
TRIAL 4	5	4
TRIAL 5	3	2
TOTAL SURVIVORS	19	11

Figure 28. Results of interspecific predator prey experiments involving *Erythemis simplicicollis*, *Pachydiplax longipennis*, and bluegill (*Lepomis macrochirus*)

greater chance of being chosen because more individuals of that species survived.

Using the Fisher Exact Test, data were still significant ($p = 0.021$) (0.05 CL) meaning that the probability of 11 *Erythemis* being eaten would occur in nature 98 percent of the time and that this event would occur by chance 2 percent of the time.

Trials were run without fish in order to examine intraspecific and interspecific competition among naiadal dragonflies. One trial examined cannibalism among naiads of different size classes of instars. After 45 hr, there was an 80 percent survival, with the smaller naiads having been decapitated (Figure 30). This was compared to another odonate species when after 72 hr several naiads had been decapitated, and after 96 hr all that remained was the largest naiad and the seven bodies of his cohorts. Cannibalism is a likely mechanism of population regulation in dragonflies that inhabit fish-free ponds (Buskirk 1989). In another trial five naiads of each species, all approximately the same size, were grouped together for 45 hr with a predator. There was a 100 percent survival for each species (Figure 30). Cannibalism is thought to operate as a density dependent form of population control in a number of organisms, increasing in frequency during periods of food scarcity or high population density (Buskirk 1989). In populations consisting of uniformly

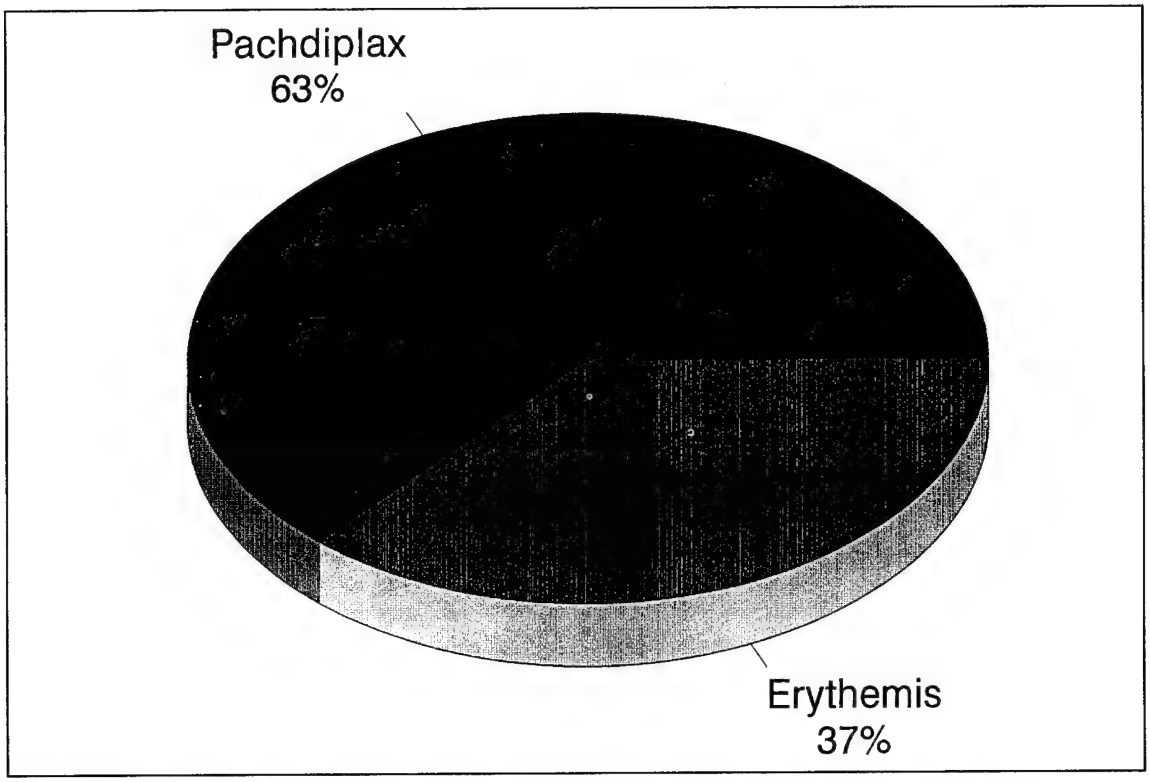
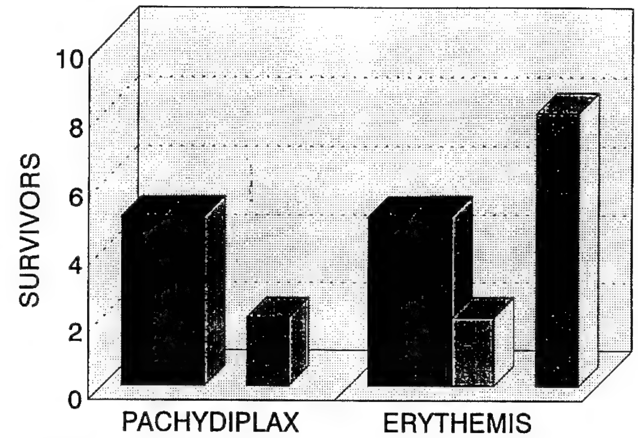


Figure 29. Graph illustrating the two-to-one ratio of surviving *Pachydiplax longipennis* to *Erythemis simplicicollis* in the predation trials involving bluegill

sized naiads, increasing density (more naiads) will cause reduced growth rates or starvation rather than increased cannibalism (Buskirk 1989). Therefore, cannibalism could help regulate only those dragonfly populations that have a variable size structure. Fish can reduce abundances of benthic macroinvertebrates, including naiadal odonates (Crowder and Cooper 1982; Morin 1984b). Several previous studies have illustrated the influence of fish on odonate population. In large-scale experiments, Crowder and Cooper (1982) demonstrated reductions in odonate density that were associated with the presence of fish. They also reported cases where active species were abundant in fishless areas but were replaced by more cryptic species where fish were present.

Morin (1984b) has documented significant effects of fish predation on both overall density and relative abundance of species in a littoral assemblage of pond-dwelling odonates. The exclusion of fish resulted in a substantial increase in odonate density in small, mesh enclosures and shifted numerical dominance from the smaller species present to a species of intermediate size.

The mechanisms by which fish alter odonate communities are not well understood. Morin's results led to the suggestion that the effect of fish predation on odonates may be size dependent. Pierce, Crowley, and Johnson (1985) determined that the effects of fish predation on odonate species may be strongly associated with behavioral patterns.



	PACHYDIPLAX	ERYTHEMIS
TRIAL 1 E.s. and P.l.	5	5
TRIAL 2 E.s. and P.l.	5	5
TRIAL 3 E.s.		2
TRIAL 4 P.l.	2	
TRIAL 5 E.s.		8

Figure 30. Results of interspecific and intraspecific predator prey experiments involving *Erythemis simplicicollis* and *Pachydiplax longipennis*

In the trial involving only one species at a time with a predator, there was a 40 percent survival for both species (Figure 30). This was compared to a study by Benke (1978) in which he stated that the primary determinant of community structure and production is an interaction between refuge level and predation rate. It is necessary for prey to be turning over at an unusually high rate, and it is possible that odonates function in stimulating the rate of prey production.

Head-width measurements. In most groups of animals, growth in weight and size is continuous. Calver (1929) emphasized that this statement is accurate for growth in weight of arthropods, but not for growth in length. Head widths have been found to give a more accurate measurement of the size and instar in odonates.

Head widths for each species ranged from 1.2 mm to 4.8 mm (Figures 31 and 32). Data indicated a univoltine life cycle for each species (Figures 31 and 32). The naiads hatch after 10 to 24 days, grow rapidly until winter, and then resume a frenzied growth in the spring until they emerge nonsynchronously all summer. Calculated growth distributions from season to season support this rapid growth from summer to fall and in the spring (Figures 31 and 32).

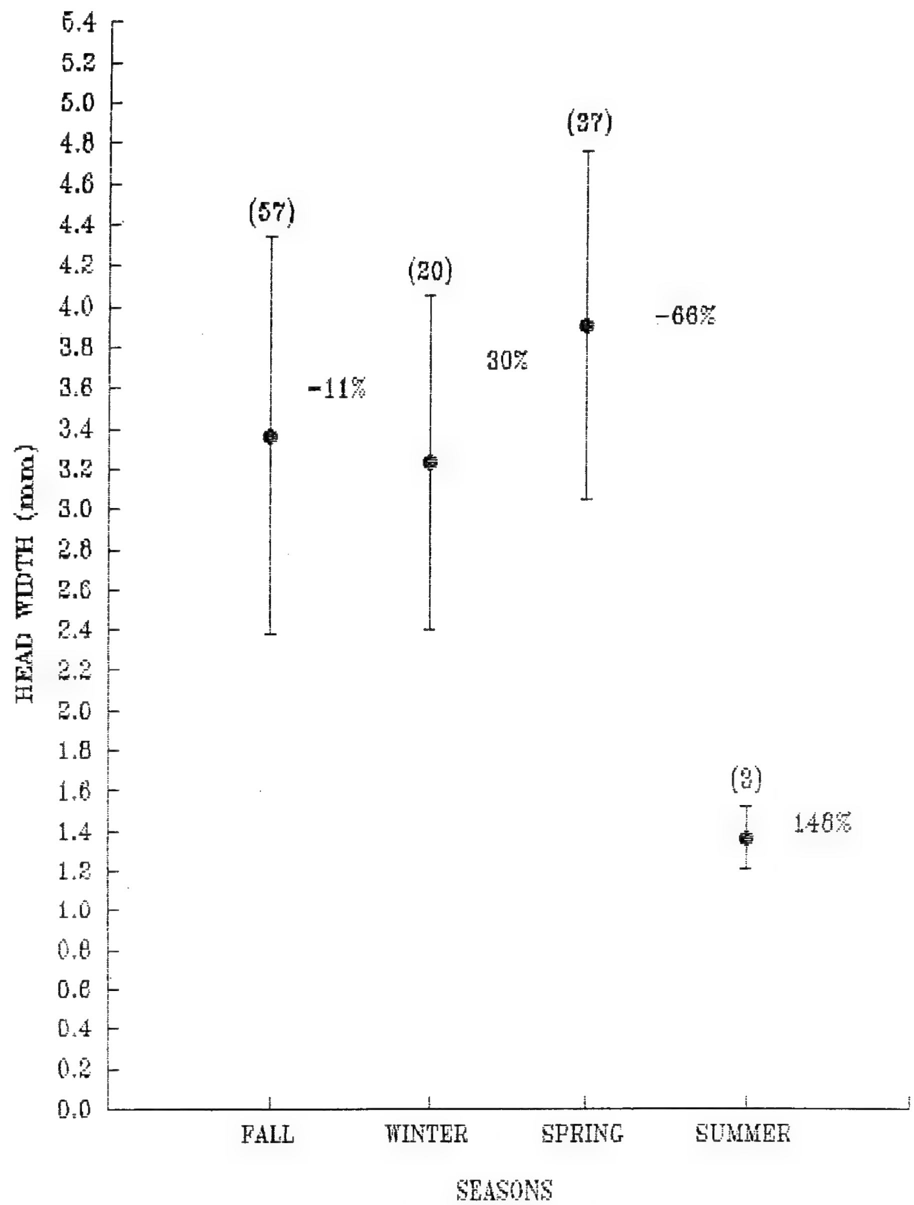


Figure 31. Head-width measurements taken from *Erythemis simplicicollis* depicted seasonally, illustrating growth distributions

Foregut and scat analyses. Eight food items were identified in the foregut analyses of *Erythemis simplicicollis* and *Pachydiplax longipennis* (Table 54). Items were placed into five major groups: *Wolffia sp.*, ostracoda, insect parts, debris, and algae. Insect parts included some identifiable remains from odonata, dipterans, and snail eggs, but for the most part, the remains were digested to an unrecognizable state. Algae included such filamentous alga as

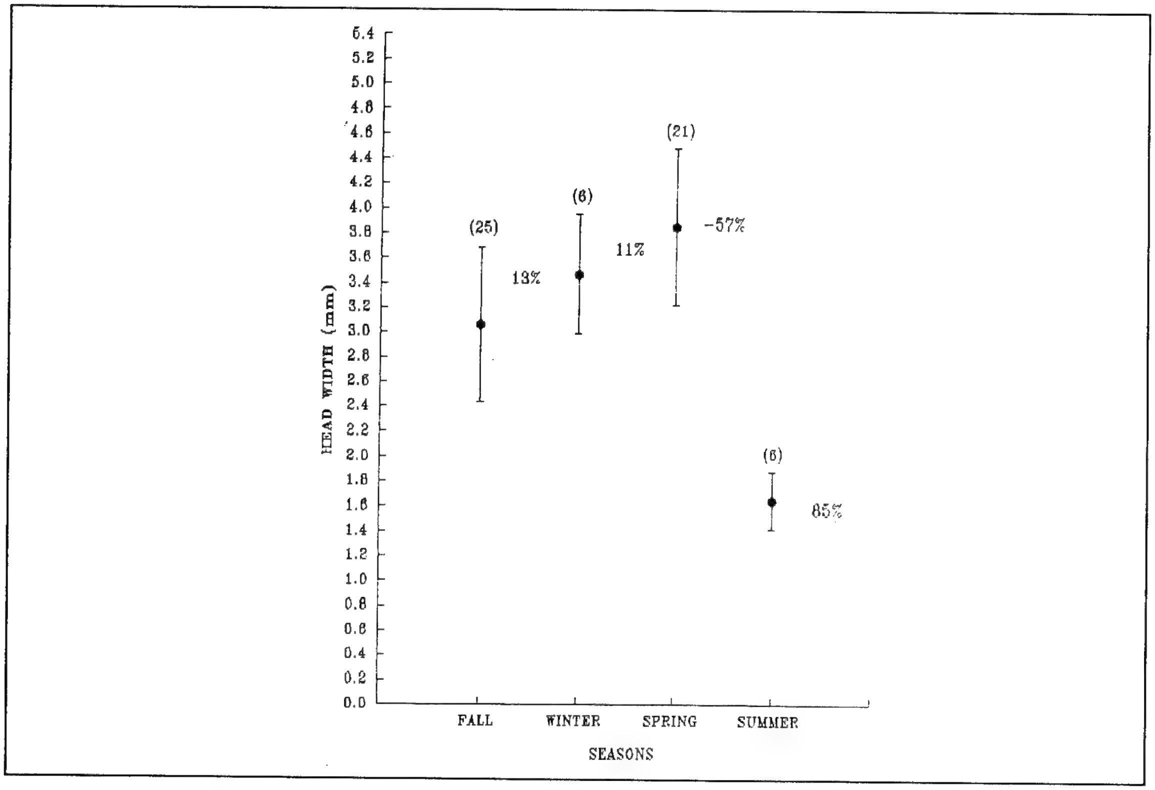


Figure 32. Head-width measurements taken from *Pachydiplax longipennis* represented seasonally, illustrating growth distributions

Table 54
Major Taxa of Food Items Found in the Foregut Analyses of *Erythemis simplicicollis* and *Pachydiplax longipennis* at GBWMA from 1992-1993

Animalia	Plantae	Detritus
Arthropoda Crustacea -copepods -ostracods Insecta -diperans -odonates Mollusca snail eggs insect parts	Plantae Clorophyta -algae Tracheophyta -*Wolffia sp.*	

Actinastrum, Mougeotia, Epithemia, and Microspora. Items were grouped seasonally for each species with various frequencies ranging from 0 percent per season to 72 percent per season with many of the items showing a variable occurrence throughout the year (Figures 33 and 34). *Wolffia sp.* is very high

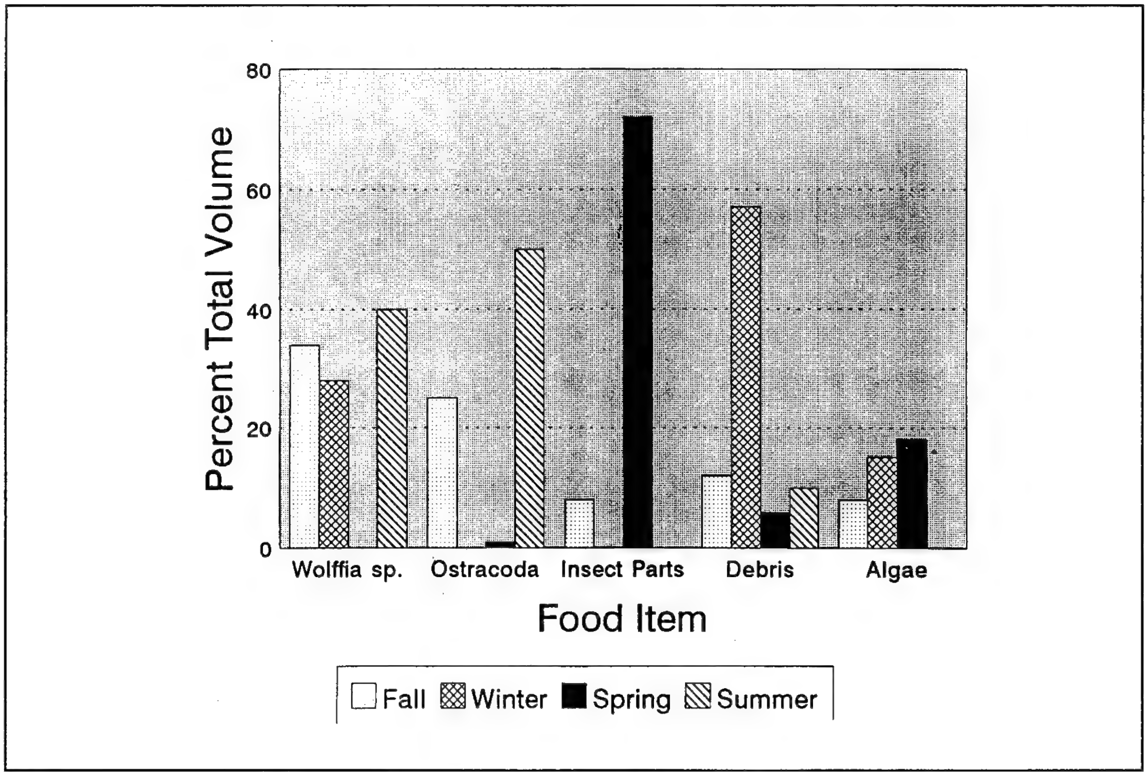


Figure 33. Results from seasonal foregut analyses of *Erythemis simplicicollis*

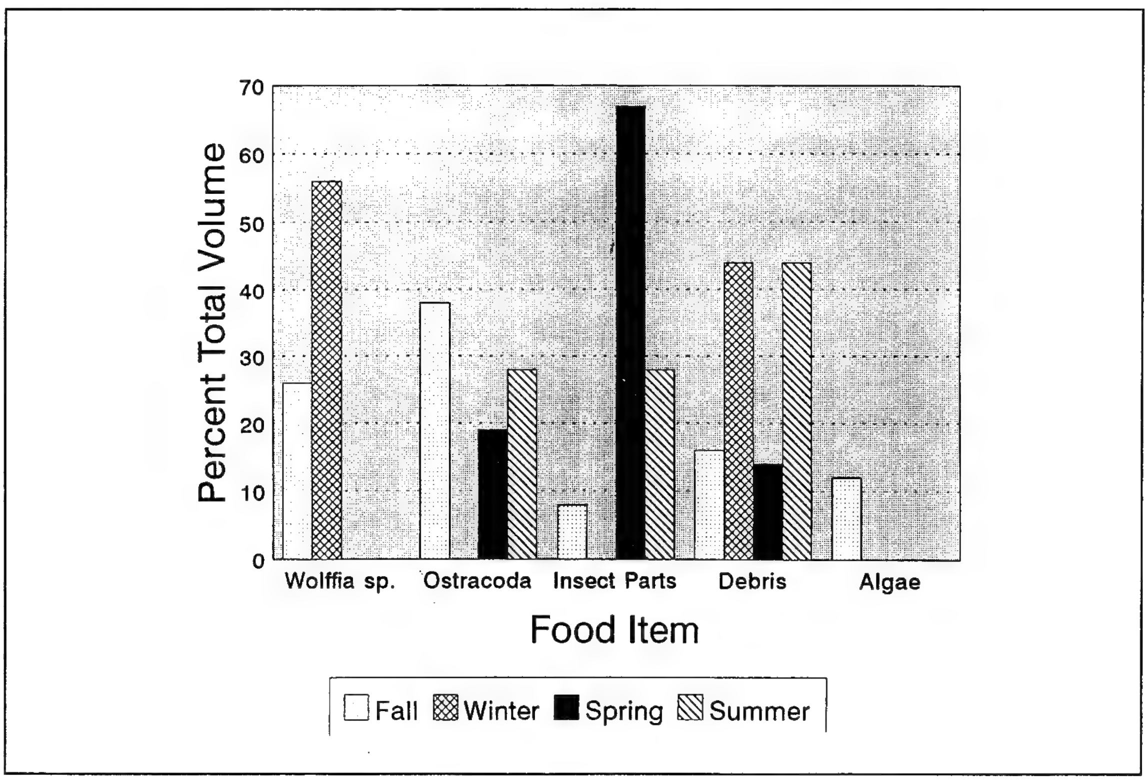


Figure 34. Results from seasonal foregut analyses of *Pachydiplax longipennis*

in the fall. This follows with the life cycle of the plant in the wetland. In the early spring, *Wolffia* starts its annual growth cycle until it reaches a full "bloom" in the late summer and early fall. It would seem from the data that the naiads are incidently taking in this "water meal" at higher concentrations when the plant is at its greatest capacity. This is in agreement with a study done by Hayes (1993) who found that the central mudminnow (*Umbra limi*) takes advantage of this explosion of growth and consumes considerable amounts of the material. The consumption of ostracoda also follows this trend, and it appears that this increase in numbers corresponds to the time frame of the increase in the *Wollffia*.

Kasimov (1956) recorded naiads feeding on oligachaetes, chironomid larva, other insects, tadpoles, frogs, fry and spawn of herring, ostracods, ticks, mites, and green alga. The most complete record to date of the natural food of anisopteran dragonfly naiads is that of Warren (1915), who examined the gut contents of 253 naiads. Warren's results show chironomid larvae and ostracods to be the commonest components of the diet.

Seasonal overlap of percent total volume presented similar values for both species using the Horn and Morisita Indices (Table 55). Percent similarity was the highest for fall versus fall and the spring versus spring, 79 and 74 percent similar, respectively (Table 55). The percent total volume of the diet is the total points awarded to a given food item divided by the total number of points awarded during the study period. This shows that although a food item may occur in many stomachs at any time, it is generally not the only item in those stomachs. Such is the case with the *Wolffia sp.* and ostracods. Although these food items occur in large number in the fall and early winter, they are not the sole food sources. The greatest percentage of empty stomachs (55 percent and 40 percent, respectively) occurred in the winter for both *Erythemis simplicicollis* and *Pachydiplax longipennis*. Libellulids are considered "summer species." They are characterized by a less synchronized emergence, a longer flight season, and diapause, if present, not occurring in the final instar. Libellulids overwinter in a great spread of instars (Paulson and Jenner 1971). The percentage of empty stomachs in the winter suggests that in the winter the naiad diapauses or comes to a growth halt.

Table 55
Horn and Morisita Index Values Including Percent Similarity Between *Erythemis simplicicollis* and *Pachydiplax longipennis*

Seasons Compared	Horn	Morisita	Percent Similar
Fall versus Fall	0.916	0.949	79.0
Winter versus Winter	0.885	0.879	72.0
Spring versus Spring	0.811	0.933	74.0
Summer versus Summer	0.554	0.483	38.0

Scat analyses did not offer any other hints to the dragonflies' diet. Ostracods were the most abundant organisms present; more importantly, some of the ostracods and protozoa passed through the digestive system alive. GBWMA is saturated with chironomids, a major component of the fecal remains found in studies by Pritchard (1964), Chutter (1961), and Corbet (1962). But, none of the foreguts examined contained any fragments to suggest that chironomids were of any importance in the dragonflies' diets.

Rearing and growth. Eggs from a *Pachydiplax longipennis* female were reared in the laboratory for 13 days. On day 14 a light was placed over the watch glass to warm the water. The eggs hatched at 19 °C, 21 days after they had been laid. The instars were preserved weekly, but after 3 weeks a fungal infection appeared and killed the remaining naiads.

Respiration. The mean oxygen consumption for the eight naiads at 19 °C was 0.19 ul/mg dry wt/hr (S.D. = 0.11) (Figure 35). The mean oxygen consumption at 11 °C was 0.15 ul/mg dry wt/hr (S.D. = 0.13) (Figure 35). The average weight of the naiads was 18.73 mg.

The calculated-t value was 5.395, while the student-t for a two-tailed test with 8 deg of freedom was 1.039 (0.05 confidence level). These calculations indicated that there was no difference in the mean of these two samples. Therefore, there was no significant difference in the two temperatures. Because of the small sample size and data from only one trial run, these results further support previous findings that as temperature increases, so do the respiration rates of the insects (Ruggles 1990). Conversely, if the temperature were lowered, the metabolic rate would decrease. In their naiadal life stage, during the harsh winter months when available nutrients are scarce, a reduced metabolism would lead to an increased chance of survival for the insects (Knight and Simmons 1975). In correlating body weight and metabolic rates, there was a significant inverse relationship. Knight and Gaufin (1966) reported that the metabolic rate is nearly proportional to the body weight and, in general, larger animals have lower metabolic rates. Therefore, temperature is not the only factor which affects the rate of oxygen consumption. More trial runs conducted with varying the temperature and pH should be done.

Low pH tolerance (LD_{50}). Although adult odonates are highly vagile and thus of limited value as pollution indicators, the naiads as a group are highly sensitive to habitat degradation. In contrast to the poor ability of fish to tolerate acid-polluted waters, insects are usually found even under the most severe conditions. The importance of insects as indicators of the degree of pollution and as herbivores and predators in the aquatic ecosystem stimulated many studies in the past to look at their distribution and diversity in acid streams (Parsons 1968; Bell and Nebeker 1969; Sheaffer and Little 1969; Warner 1971; Roback and Richardson 1971; Bell 1971; Weed and Rutschky 1972; Koryak, Shapiro, and Sykora 1972; and Roback 1974. Other studies focused on the effects of acid streams on aquatic insect diversity and biomass (Tomkiewicz and Dunson 1977, Havas 1980). The problem of acidosis in the streams and

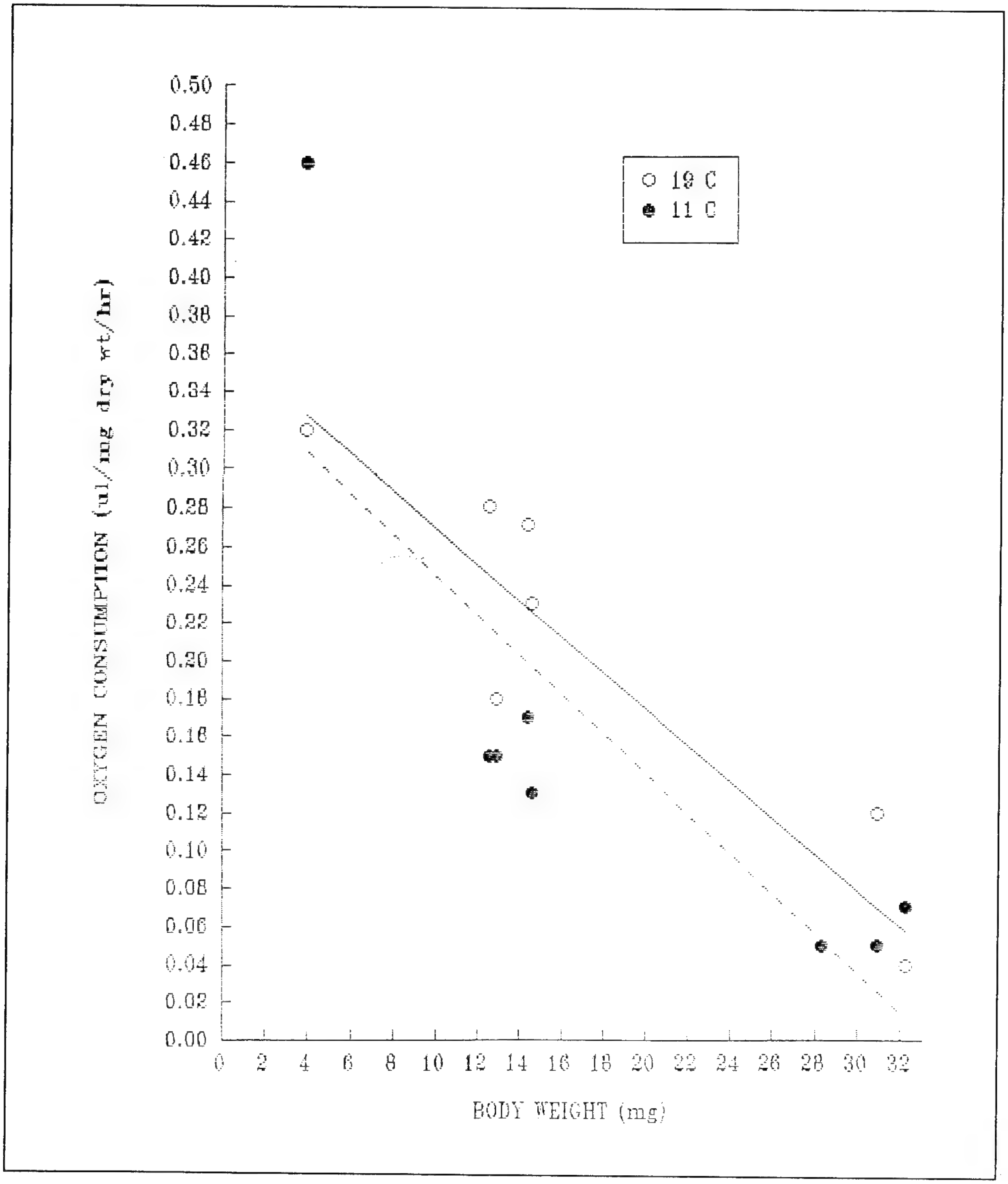


Figure 35. Rates of oxygen consumption for *Erythemis simplicicollis* at 11 °C and 19 °C

watersheds stems from the burning of fossil fuels which emit sulphur dioxide and nitrogen oxides into the atmosphere. These oxides produce sulfuric acid and nitric acid which are returned to the streams through precipitation. In the bituminous coal fields of West Virginia, the 7.5 tons of coal that are mined annually cause widespread pollution in the form of acid mine drainage (AMD) (Minerals Yearbook 1969). Huntington is indirectly affected by these pollution problems. The Ohio River drainage is directly affected by runoffs which in

turn could affect GBWMA by excessive flooding from the Ohio River. Therefore, it was interesting to look at the acid tolerance LD_{50} (lethal dosage for 50 percent survival) of one of the more abundant odonates at GBWMA to determine whether *Pachydiplax longipennis* would be a good early detector of low pH.

After 96 hr, the TLm or LD_{50} for *Pachydiplax longipennis* was calculated using the straight-line graphical interpolation method. The TLm is the pH at which there is a 50 percent survival after 96 hr. The TLm for *Pachydiplax longipennis* was calculated to be 2.17 (Figure 36). This figure was considerably lower than indicated in any of the previous studies involving odonates. Bell and Nebeker's (1969) studies found that the dragonfly species, *Boyeria vinosa*, could not tolerate lower than 3.25 for even short periods of time. Field data of Warner (1971) and Bick, Hornuff, and Lambremont (1953) indicate that *Boyeria vinosa* is tolerant of these low pH values at least for short periods. Another dragonfly, *Ophiogomphus rupinsulensis*, was found by Bell and Nebeker (1969) to be only moderately tolerant. It has been reported from areas where acid pollution is a problem. Like *Boyeria vinosa*, *Ophiogomphus rupinsulensis* could probably tolerate low pH values if they were of short

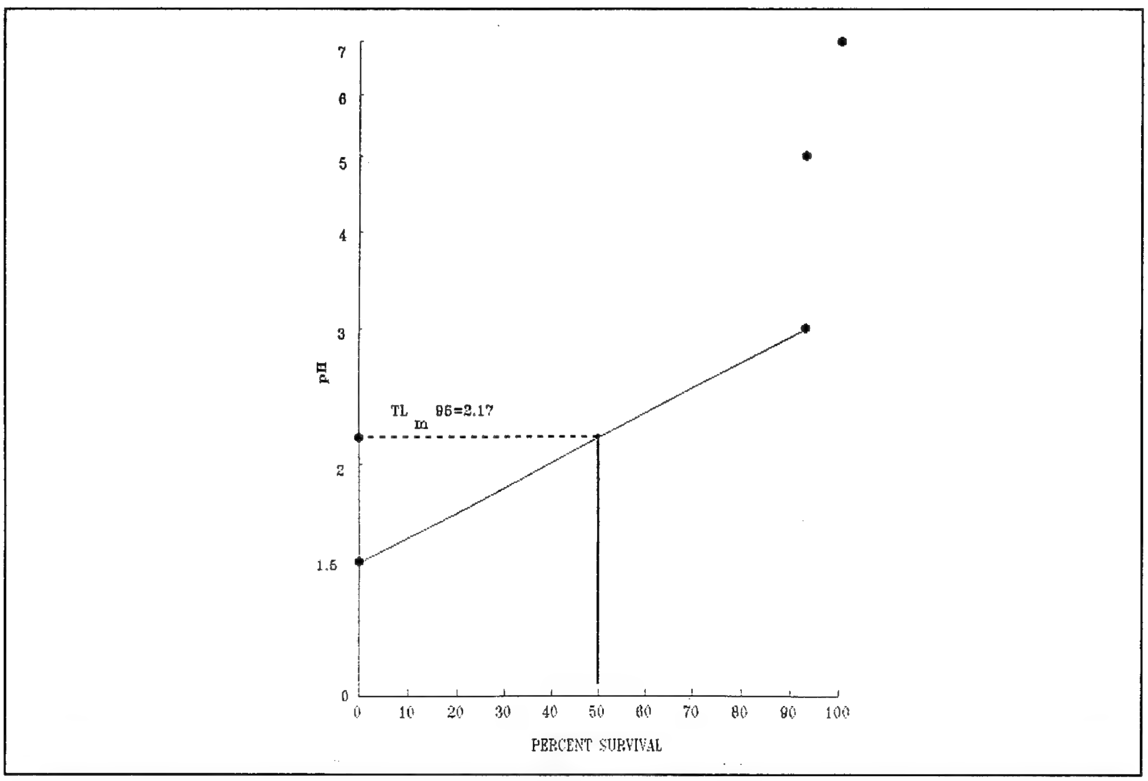


Figure 36. Calculated TLm for *Pachydiplax longipennis* using the straight-line graphical interpolation method

duration. Apparently, the dragonflies were some of the most numerous organisms in the acid investigation by Bick, Hornuff, and Lambremont (1953), in a stream whose pH ranged from 4.0 to 6.8.

Following the 96-hr or acute-static bioassay, the survivors were maintained at the standard pH values for 72 more hr for completion of a short-term chronic-static bioassay. One hundred percent survival was found at pH 7.0 for the 168-hr short-term chronic testing (Table 56). Ninety-three percent survived at pH 5.0 after 48 hr, but this was probably due to handling or stress incurred before the experiment was started. Ninety-three percent survived at pH 3.0 for 24 hr, which was also probably due to causes other than acidosis; the 93 percent survival was maintained until 168 hr when it dropped to 81 percent. No survivors were found at pH 1.5. Therefore, the TLm of 2.17 was tested. After 48 hr, 50 percent of the naiads were dead; after 96 hr, there were no survivors. This proves that the calculated TLm was close, but that the pH generated from the linear regression, 2.9, may have actually been more accurate (Figure 37).

Table 56
Percent Survival of *Erythemis simplicicollis* During Short Term Chronic Toxicity Testing at pH Values of 1.5, 3.0, 5.0, and 7.0

pH	24 Hr	48 Hr	72 Hr	96 Hr	168 Hr
7.0	100	100	100	100	100
5.0	100	100	93	93	93
3.0	100	93	93	93	81
1.5	0	0	0	0	0

Summary and Conclusions

The low dissolved oxygen and slightly alkaline conditions at GBWMA seem to provide suitable habitat for five of the nine adult dragonflies recorded from October 1992 to October 1993. *Erythemis simplicicollis* and *Pachydiplax longipennis* are the most abundant species. Head-width measurements taken from *Erythemis* and *Pachydiplax* denoted a univoltine life cycle, extraordinary growth from summer to fall, and a nonsynchronous pattern of emergence from May until October. Other naiads found to exist at GBWMA were *Anax junius*, *Plathemis lydia*, and *Tramea lacerata*. Adults of *Libellula cyanea*, *L. pulchella*, *L. luctuosa*, and *Sympetrum vicinum* were collected during the summer months of 1993, but the naiads of these species were never collected. Unless these naiads are occupying a habitat within the swamp that was not dredged, the eggs that are deposited by these adults must be unable to survive or are consumed by a predator. Also, migration from the Ohio River, streams, or ponds could account for the presence of adults and the absence of naiads.

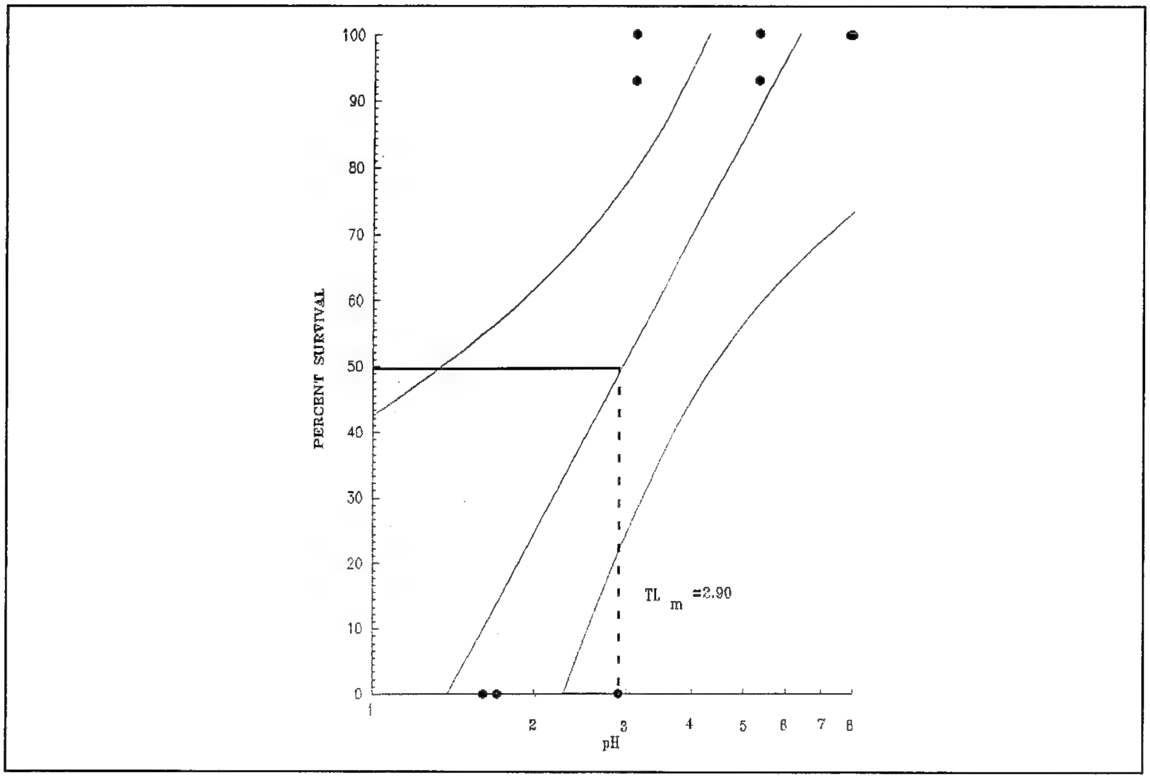


Figure 37. Calculated TLm using linear regression for *Pachydiplax longipennis*

Predation can be an important regulatory mechanism during the naiadal phase of the odonate complex life cycle. Fish greatly reduce the number of naiads making the successful transition between the aquatic naiadal phase and the terrestrial/aerial adult phase of the life cycle (Morin 1984b).

In Morin's (1984b) experiment, competition among dragonfly naiads occurred only at elevated densities produced by excluding fish, suggesting that fish predation may keep dragonfly densities below the level where competitive interactions are detectable. If this phenomenon is a general one, it might be expected that competition among naiadal odonates would be more prevalent in small, temporary, or otherwise fishless ponds (Pierce, Crowley, and Johnson 1985).

Cannibalism can be a very responsive regulatory agent by adjusting the population size directly to its food supply and by exerting instantaneous effects on density (Buskirk 1989). This means of population regulation may be particularly effective for predators inhabiting temporary ponds in which food supply and density can fluctuate dramatically and unpredictably with changes in water level.

Interactions among odonates and with their predators are complex, and more experiments will be necessary to assess the relative roles of biotic interactions in these communities.

In summary, successful mating and the assurance of offspring in dragonflies are accomplished by the following:

a. Males and females exercise the same habitat selection for the mating site and have approximately the same seasonal and daily rhythms of reproductive activity.

b. Although accurate spatial and temporal concurrence are important factors in maintaining sexual isolation, visual recognition seems to be most significant.

c. Uninterrupted copulation can be achieved by:

(1) Males becoming localized and spaced out as a result of their aggressive behavior.

(2) The duration of copulation being very short.

(3) The mating pair leaving the breeding site and settling on a suitable substrate in or around the water.

d. Male interaction provides an effective means of sexual selection for male maturity, vigor, and potency. Since males are deficient in these attributes, they are correspondingly less able to resist displacement by other males at the mating site.

e. Protection of the ovipositing female against predation may sometimes result from the male arriving early at the site and testing it for safety. Protection of the ovipositing female against male interference is achieved by:

(1) Territorial behavior.

(2) The males arriving at the breeding site earlier than females and therefore achieving stability.

(3) The male guarding or remaining in tandem with the ovipositing female.

(4) The female not being recognized by males while ovipositing.

(5) Oviposition occurring at a time or place other than at the mating rendezvous.

f. Laying the eggs in a site suitable for survival of the aquatic stages depends upon the ability of the female and male to select the appropriate microhabitat.

g. Overpopulation of the breeding site is moderated by male interaction and by females being driven away when male competition is intense (Corbet 1962).

The food of dragonfly naiads is broken up by the mouthparts and is stored for some time in the crop before passing slowly through the gizzard. The gizzard has little effect on larger chitinous pieces, but it grinds up the softer material. This makes identifying the foregut or fecal remains of dragonflies a very tedious job. The 10 food items found in the foreguts of *Erythemis simplicicollis* and *Pachydiplax longipennis* were very similar between both species from season to season, indicating a competition for the same prey. However, because naiads are general animal feeders and will strike at any moving prey below a certain size, their diets should be proportional to the relative abundance of animals in the environment. Therefore, taking large samples of possible prey items over a long period of time may serve as a more accurate indicator of naiadal diets.

Respiration studies on the naiads indicated that as temperature increases, oxygen consumption increases. This is attributable to an increased metabolic rate. Also, there was a significant inverse relationship between body weight and oxygen consumption. Larger or more mature naiads have a slower metabolic rate or reduced oxygen consumption.

There was no previous literature on the effects of acid pollution on the dragonfly *Pachydiplax longipennis*. *Pachydiplax* had a calculated TLm of 2.17, comparable to Bell and Nebeker's (1969) study in which their most tolerant species, a caddisfly (*Brachycentrus americanus*), had a TLm of 1.5. In all of the previously conducted bioassays, however, the test organisms died at pH values below those normally found in the field. Conditions in the field differ from those in the laboratory, and ecological factors exist in the streams which may alter the results, but the values given do constitute a valid comparison between the relative toxicity of the low pH tested and the tolerance of the test organism. In general, aquatic insects are tolerant of acid conditions, at least for periods of less than 1 week. Future work should deal with long-term effects on molting, growth, and reproduction, as well as survival for a specified period of time.

9 Preliminary Observations on the Reproductive Biology of the Grass Pickerel, *Esox americanus vermiculatus* LeSueur[1]

Introduction

Objectives

The grass pickerel, *Esox americanus vermiculatus* LeSueur, is mentioned as Undetermined on the Vertebrate Species of Concern List in West Virginia (WVDNR 1987). The reason for the status is the lack of West Virginia data and the habitat destruction of the lentic, vegetated spawning area by agricultural, residential, and industrial developments (i.e., via pond and lake construction and habitat drainages and fillings).

Grass pickerel require flooded vegetation for spawning and nursery area for the young-of-the-year (YOY). Green Bottom Swamp, a naturally occurring wetland, provides excellent habitat for their spawning activities. This type of habitat is a rarity, accounting for less than one percent of the state's total surface area, in otherwise mountainous West Virginia. Additionally, personnel at the U.S. Army Corps of Engineers, Huntington District, are adding new marshland (mitigation site) by building dykes at the downstream end of the property and pumping water from the Ohio River to fill them. Data from this investigation will provide information aiding in management strategies relating to grass pickerel. Further, little spawning or developmental information is available on the grass pickerel throughout its range (Wallus et al. 1990). The objectives of this investigation were as follows:

[1] Donald C. Tarter, Ph.D.; Ronald C. Tipton, M.S.

a. To elucidate the spawning activities of the grass pickerel at GBWMA.

b. To establish baseline data for managing the reproductive activities of the local population.

c. To determine any reproductive activities at GBWMA.

d. To enhance the data base on the "Undetermined" status of the grass pickerel in West Virginia.

Study area

Buttonbush *(Cephalanthus occidentalis)*, a small wetland shrub, dominates the deepest and wettest areas of GBWMA, while *Lemma minor, Spirodela polyrhiza* and *Wolffia.* sp. cover the surface water. *Carex* and *Juncus* spp. thrive in the swamp on the soft, marsh soil.

Taxonomy and Distribution

Taxonomy

The family Esocidae contains a single genus *Esox* which includes five extant species (Nikolski 1961): *Esox reicherti* Dyboski (Amur pike), *E. masquinongy* Mitchell (muskellunge), *E. lucius* L. (northern pike), *E. niger* LeSuiur (chain pickerel) and *E. americanus* Gmelin (redfin pickerel). *Esox americanus* was reported to include the two subspecies, *E. a. americanus* Gmelin (redfin pickerel) and *E. a. vermiculatus* LeSueur (grass pickerel) Legendre 1954). Legendre's classification was accepted in the American Fishery Society Special Publication No. 6 (1970) and is the basis for the sub-specific designation in this report.

Distribution

The grass pickerel ranges from east Texas up the Mississippi River basin to southern Canada and the Great Lakes, east from Oklahoma to the eastern coast of North America (Clay 1975, Trautman 1981, Wallus et al. 1990). In West Virginia, the distribution is limited to four counties (Cabell, Jackson, Mason, and Wayne) along the Ohio River in the southwestern region. Its preferred habitat is clear, slow moving heavily vegetated waters such as marshes, back channels, oxbows, and bogs (McClane 1965, Trautman 1981, Pflieger 1975). The highest population densities are found in shallow, weedy areas with plants such as leafy liverworts, pondweeds, water lilies, filamentous algae, and broad-leaf cattails (Becker 1983).

Habitat

McClane (1965) reported that the grass pickerel prefers a shallow, low gradient environment with a soft bottom which is covered with a heavy growth of aquatic vegetation. Trautman (1981) reported the grass pickerel to occur in marshes, bog ponds, oxbows, and slow moving streams in Ohio.

Methods and Materials

Field studies

Collections. Seasonal collections of grass pickerel were made on the following dates (number of fish in parenthesis): Winter/26 February 1993 (2); Spring/ 21 April 1993 (48); Summer/20 July 1993 (21); and Fall/20 October 1993 (16). The area was ice covered most of the winter season. Methods of collection included traps, seines, and electrofishing. Most grass pickerel were collected with seines. They were stored on ice and later preserved in 10-percent formalin.

Water quality and temperature. On each seasonal collection date, temperature (°C) and the following water quality parameters were measured using a Hach chemical kit, Model 36-WR: dissolved oxygen (mg/L), alkalinity (mg/L $CaCO_3$), CO_2 (mg/L), total hardness (mg/L $CaCO_3$), total acidity (mg/L), and pH. Temperatures were measured with a maximum-minimum thermometer.

Spawning. In an attempt to observe spawning activities, 21 trips were made to the swamp between 28 February and 18 April 1994.

Larvae and juveniles. Several attempts were made to collect larvae and juveniles (>22 mm TL) in the field during March and April (1993, 1994). Long-handed, fine mesh dredges were used to sample the aquatic vegetation.

Laboratory studies

Fecundity. The number of eggs was estimated using the volumetric method (Lagler 1956). A sample of eggs was blotted dry on a paper towel. The volume of the sample was obtained by water displacement in a burette. Similarly, the volume of the entire lot of eggs, including the sample, was obtained in a burette. The total number of eggs was estimated by the following equation:

$$X:n = V:v \qquad (11)$$

where

X = unknown total number of eggs in the lot

n = number counted in the sample

V = total displaced volume of all eggs

v = volume of sample

Since only one sexually mature female was collected during the first year, attempts will be made to obtain more females for a linear regression analysis with total length.

Sexual maturity. Only one sexually mature male and one female were collected during the study period, on 26 February 1993. The female contained primary (mature), secondary, and tertiary eggs. Total lengths were measured with a standard fish-measuring board.

Gonosomtaic index (GSI). To determine the seasonal GSI, gonads were removed from 32 grass pickerel. They were blotted dry on a paper and weighed on a Mettler balance (nearest 0.001 g). Similarly, the grass pickerel was blotted dry and weighed on the balance (nearest 0.01 g). The GSI was determined by dividing the gonad weight by the body weight (×100). Sex was determined on the grass pickerel collected in fall and winter seasons. Sex will be determined later using histological preparations on the grass pickerel in the spring and summer seasons.

Egg diameters and incubation. To determine the egg diameters, 50 primary eggs (mature) were removed from an ovary. The eggs were separated and measured with a dial vernier caliper (nearest 0.001 mm). Based on the primary (mature) eggs in the sexually mature female and the appearance of larval fish in the field, the length of the incubation period was estimated for the local population.

Seasonal histology. Histological preparations of the testes and ovaries will be made during the fall (1994). These preparations will help determine the spawning activities of the local population of grass pickerel.

Meristics and morphometrics. To determine sexual dimorphism in the population, several meristic (counts) and morphometric measurements will be made during the summer (1994). ANOVA and t-test will be used to analyze the data.

Sex ratio. A chi-square test will be used to determine any deviation from the 1:1 sex ratio (0.05 confidence level). This test will be performed after the sex has been determined for all grass pickerel.

Spawning. An attempt will be made during the spawning season (1995) to collect mature males and females for observation on spawning behavior in a "living stream." The water temperature will be controlled at the threshold temperature for spawning.

Results and Discussion

Field studies

Water quality and temperature. The water quality parameters are summarized in Table 57. The water temperature in Green Bottom Swamp fluctuated from 0.0 to 27.8 C, winter (February) and summer (July), respectively; the mean was 13.9 °C. Ice covered the area for portions of January and February. Dissolved oxygen values ranged from 2 to 6 mg/L, summer and winter, respectively; the mean was 4.3 mg/L. Total acidity was zero in all seasons. Carbon dioxide values ranged from 10 to 20 mg/L, fall and spring/winter, respectively; the mean was 16.3 mg/L. Total alkalinity values ranged from 51 to 102 mg/L $CaCO_3$, summer and spring, respectively; the mean was 85.0 mg/L $CaCO_3$. Total hardness values ranged from 102 to 123 mg/L $CaCO_3$; the mean was 11.6 mg/L $CaCO_3$. The pH ranged from 6.5 to 8.0, fall and winter, respectively; the mean was 7.1. In most cases, the values fell within an accepted seasonal range.

Table 57
Seasonal Water Quality and Temperature Data from GBWMA, 1993

Parameters	Seasons			
	Winter (Feb.)	Spring (April)	Summer (July)	Fall (Oct.)
Temperature, °C	0.0	17.8	27.8	10.0
Dissolved oxygen mg/L	6	4	2	5
Total acidity, mg/L	0	0	0	0
Carbon dioxide mg/L	20	20	15	10
Alkalinity mg/L $CaCO_3$	102	119	51	68
Total hardness mg/L $CaCO_3$	119	123	119	102
pH	8.0	7.2	6.7	6.5

Spawning. No spawning act of the grass pickerel was observed during the study periods (1993, 1994). Apparently, the spawning activities are very secretive. No collections of naturally spawned eggs are known from the Ohio River drainage (Wallus et al. 1990). Another attempt will be made to observe the spawning act during the spawning season in 1995.

According to Raney (1959), single females were accompanied by several males during the spawning act. Eggs and milt were ejected at intervals by lashing of caudal fin. Eggs were broadcast over vegetation (Crossman 1962). No nest building or parental care of young-of-the-year were recorded in the grass pickerel (Scott 1954; Ming 1968).

Early spawning is thought to be an adaption for highly piscivorous fishes such as the grass pickerel. The larval and juvenile fishes are thought to feed on the larvae of later-spawning fishes. This hypothesis will be tested in the laboratory and field studies during this investigation.

Location. It is suspected that spawning occurs in the aquatic vegetation associated with buttonbush. Generally, grass pickerel spawn over aquatic vegetation, moss, leaves, and twigs in sloughs, temporary flood plains, marshes, and shallow vegetated pools of tributary streams (Kleinert and Mraz 1966, Crossman 1962, and Scott and Crossman 1973). Sometimes grass pickerel migrated from lakes into small streams for spawning activities (McNamara 1937).

Season. Apparently spawning occurred in late February or early March in GBWMA. A sexually mature male and female were collected in a trap on 26 February 1993.

McNamara (1937) reported that the grass pickerel is one of the earliest fish to spawn in spring. Larval collections from the Big Sandy River in Tennessee in early April suggested a late February to March spawn (Wallus et al. 1990). Ming (1968) reported that grass pickerel spawned in late February to March in Oklahoma, while Kleinert and Mraz (1966) noted a mid-March to mid-April spawning season in Wisconsin. A second, low-intensity spawning period was reported in summer or fall in Michigan (Lagler and Hobbs 1943).

Temperature. Based on field data, the threshold temperature for spawning in GBWMA is approximately 9 °C. This temperature was first recorded on 25 February 1994 and again on 6 March 1994.

Crossman (1962) reported that grass pickerel spawned between 7.8 to 12.2 °C in Ontario, Canada. In Wisconsin, grass pickerel spawned between 4.4 to 11.7 °C (Kleinert and Mraz 1966), while they spawned at <18.3 °C in Oklahoma (Ming 1968). In other studies in Canada, grass pickerel spawned between 4 to 12 °C (Scott and Crossman 1973).

Larvae and juveniles

Despite several searches in the aquatic vegetation, no yolk-sac larvae (6 to 10 mm TL) were found during the post spawning period. Yolk-sac larvae of grass pickerel attached to vegetation in Canada (Scott and Crossman 1973). Ming (1968) reported yolk-sac larvae among the leaf litter in winter in Oklahoma. An attempt will be made to find the yolk-sac larvae in 1965.

Although the aquatic vegetation was searched several times, no post yolk-sac larvae (11 to 21 mm TL) of the grass pickerel were found after the yolk-sac larval stage. Mansueti and Hardy (1967) found post yolk-sac larvae in very shallow water in roadside ditches and overflow pools of moderate to large rivers. Ming (1968) collected post yolk-sac larvae among dead leaf litter in Oklahoma. An attempt will be made to collected the post yolk-sac larvae in 1995.

The first juvenile grass pickerel (24.2 mm TL) was collected in aquatic vegetation on 10 March 1993. On 21 April 1993, 43 juveniles, ranging in size from 22.9 to 67.5 mm TL ($\bar{X}$ = 37.3 mm TL), were collected from thick beds of *Potamogeton crispus*. Kleinert and Mraz (1966) reported the nursery area for juveniles in a weed-choked slough. Wallus et al. (1990) recorded juveniles in floodplain pools and sloughs of a Tennessee River tributary among dense aquatic vegetation.

Laboratory studies

Fecundity. The fecundity of an individual female fish depends on several different factors including her size, age, and condition (Lagler, Bardach, and Miller 1962).

Only one sexually mature female was collected during the study (26 February 1993). Based on the volumetric method, the number of primary (mature) eggs was 3,167.

Crossman (1967) reported an average of 756 mature eggs from grass pickerel in Ontario, while Kleinert and Mraz (1966) noted a range of 843 to 4,584 mature eggs in Wisconsin. Carbine (1944) recorded 803 mature eggs (total eggs = 15,732) from a grass pickerel in Michigan. An attempt will be made to collect additional sexually mature females during the spawning season in 1995.

Sexual maturity. Since only one sexually mature male and one female grass pickerel were collected, limited information is available on sexual maturity at this time. The total lengths were 240 and 280 mm, male and female, respectively.

Ming (1968) reported grass pickerel sexually mature at age 1 year at 109 mm TL for females and 188 mm TL for males in Oklahoma. Kleinert and

Mraz (1966) recorded both sexes of grass pickerel sexually mature at 108 mm TL, while McCaraher (1960) noted sexual maturity at 102 mm TL in Nebraska. In Canada, the grass pickerel was sexually mature by 2 years of age at 141 mm TL for males and 157 mm TL for females (Crossman 1962). An attempt will be made to collect additional sexually mature grass pickerel in 1995 for TL measurements.

Gonosomatic index (GSI). Grass pickerel were divided into three groups: males (October, February), females (October, February), and juveniles (April, July). Gonads removed from grass pickerel in the spring (April) and summer (July) could not be sexed without histological preparations. Gonads could be sexed in the fall (October) and winter (February) collections. In the fall season, the average of the ratios was 0.022 and 0.011 percent, females (N = 5) and (N = 11), respectively (Table 58, Figure 38). The GSI for the winter season (February) was based on only one male and female grass pickerel. The GSI was 4.31 and 0.34 percent, female and male, respectively (Table 58, Figure 38). On that basis, it was obvious that the sex products of each sex became ripe at about the same time. The ratios declined rapidly in the spring (April) collection; the mean was 0.002 percent (N = 5) (Table 58, Figure 38). No increase in the ratio was noted in the summer (July) season (0.002 percent) (N = 9) (Table 58, Figure 38). The first marked increase in the ratio between gonad weight and body weight in winter (February) was interpreted as the onset of the reproduction season. An attempt will be made in 1995 to collect more males and females from the winter season. No information was found in the literature regarding the GSI in grass pickerel.

Egg diameters and incubation. Hickling and Rutenberg (1936) indicated that the duration of the spawning season can be ascertained by recording the diameters of the eggs as they develop within the ovary.

In GBWMA, the average diameter of eggs (N = 5) from a female pickerel collected on 26 February 1993 was 1.79 mm (range, 1.40 to 2.15 mm).

Kleinert and Mraz (1966) reported that mature ovarian eggs were 1.5 to 2.4 mm in diameter in grass pickerel from Wisconsin, while Crossman (1962) found an average of 1.4 mm in diameter from ovarian eggs in grass pickerel from Ontario. Leslie and Gorrie (1985) recorded an average of 2.8 mm (range 2.5 to 3.0 mm) in diameter from grass pickerel. Fertilized eggs are transparent and amber-to-yellow in color, demersal, adhesive or nonadhesive (Kleinert and Mraz 1966; Crossman 1962; and Raney 1959). Eggs are probably scattered among aquatic vegetation (Crossman 1962).

The estimated incubation time for eggs developing in GBWMA was 8 to 12 days at 9 to 10 °C. This estimation is based on a sexually mature collection on 26 February 1993 and field collections of larval and juvenile pickerel.

Table 58
Seasonal GSI of Grass Pickerel Collected at GBWMA, 1993

Date	Opercle Tag No.	Sex[1]	Body Wt., g	Gonad Wt., g	GSI
26 Feb	1	F	118.60	5.1147	4.3126
	2	M	90.20	0.3057	0.3389
21 April	3	J	80.49	0.5062	0.0062
	4	J	82.16	0.0820	0.0009
	5	J	30.67	0.0775	0.0025
	6	J	21.92	0.0072	0.0003
	7	J	9.25	0.0182	0.0019
	8	J	42.82	0.1203	0.0028
	9	J	46.75	0.118	0.0025
	10	J	51.37	0.1374	0.0026
20 July	11	J	49.47	0.1205	0.0024
	12	J	49.27	0.0163	0.0002
	13	J	47.46	0.0148	0.0003
	14	J	38.91	0.012	0.0003
	15	J	36.25	0.1056	0.0029
	16	J	42.90	0.0092	0.0002
	17	F	36.31	0.9863	0.0271
	18	M	14.78	0.1054	0.0071
	19	M	26.05	0.2387	0.0091
	20	M	10.27	0.2178	0.0212
	21	M	13.63	0.1216	0.0089
	22	M	10.88	0.0825	0.0075
	23	F	12.99	0.2871	0.0221
24 Oct	24	M	11.86	0.1488	0.0125
	25	M	10.93	0.1132	0.0103
	26	M	8.74	0.0727	0.0083
	27	F	7.86	0.1699	0.0216
	28	M	9.10	0.1124	0.0123
20 Oct	29	M	8.50	0.0928	0.0109
	30	F	6.72	0.1445	0.0215
	31	F	7.36	0.1226	0.0166
	32	M	5.68	0.0587	0.0103

[1] M = male, F = female, and J = juvenile.

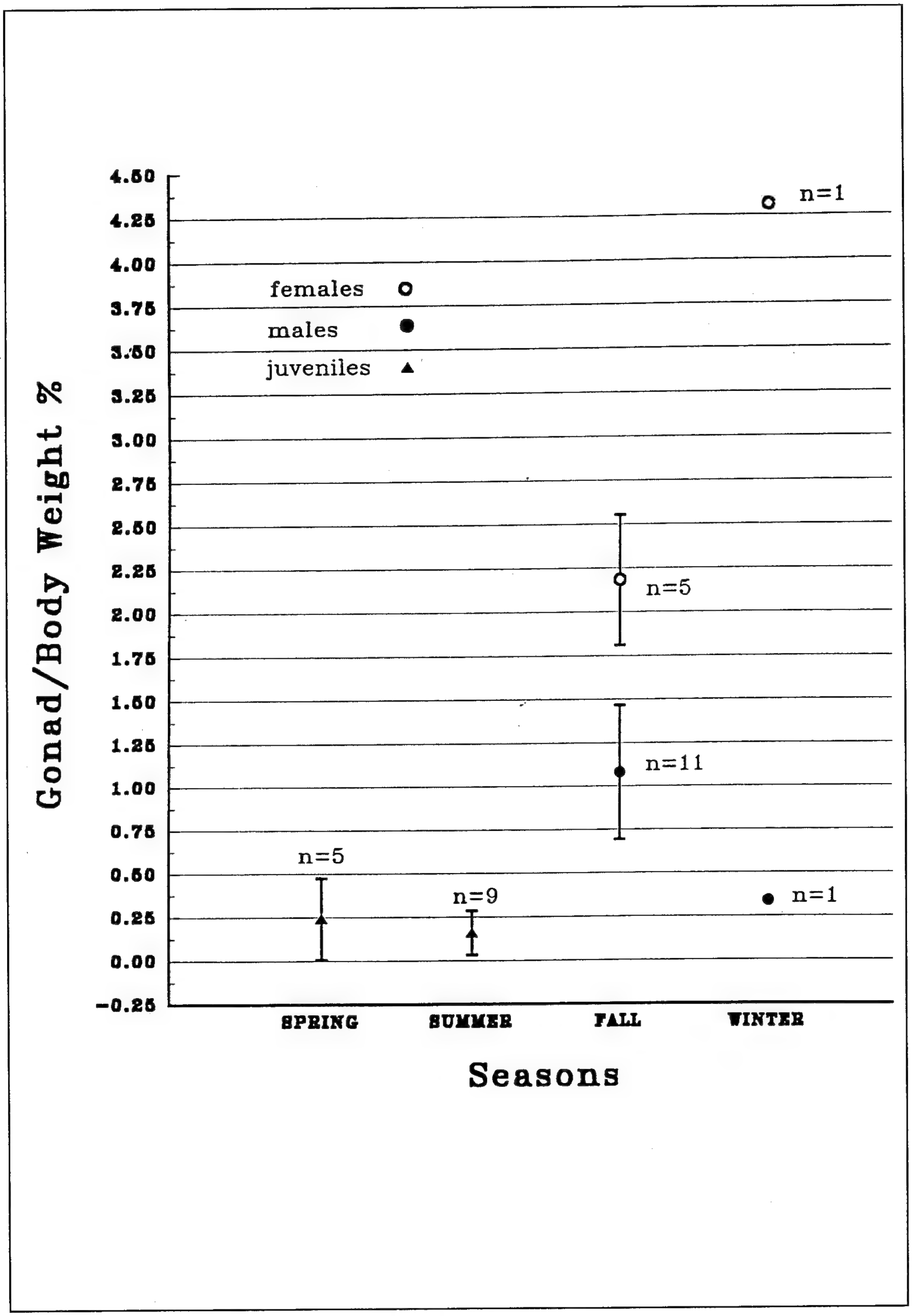


Figure 38. Seasonal GSI of grass pickerel at GBWMA

Kleinert and Mraz (1966) reported 11 days (8.9 °C), 14 days (8.3 °C) and 15 days (7.8 °C) as incubation time from grass pickerel in Wisconsin. Leslie and Gorrie (1985) noted a 12-day incubation period with eggs from grass pickerel.

Seasonal histology. Results from the seasonal histological preparation will be presented in the final report (1995).

Meristics and morphometrics. Results from the meristic (counts) and morphometric measurements will be presented in the final report (1995).

Sex ratio. Results from the chi-square tests regarding the sex ratio will be presented in the final report (1995).

Spawning. Results from the laboratory experiment on spawning activities will be presented in the final report (1995).

Summary

Preliminary observations were made on the reproductive biology of the grass pickerel in GBWMA from 1993 to 94. The shallow, low gradient environment with flooded vegetation is excellent for spawning and nursery areas for young-of-the-year grass pickerel.

Seasonal collections were made on the following dates (number of fish in parenthesis): Winter/26 February 1993 (2); Spring/21 April 1993 (48); Summer/20 July 1993 (21); and Fall/20 October 1993 (16).

Actual spawning was not observed during the reproduction season but is believed to have occurred in the aquatic vegetation associated with buttonbush in late February or early March. One sexually mature male and one female were collected on 26 February 1993. The threshold temperature for spawning is approximately 9 °C.

No yolk-sac (6 to 10 mm TL) or post yolk-sac larvae (11 to 21 mm TL) were found during the post spawning period. One juvenile (24.2 mm TL) was collected on 10 March 1993, and 43 juveniles (22.9 to 67.5 mm TL; $\bar{X}$ = 37.3 mm TL) were found on 21 April 1993. The nursery area for the juveniles was the thick bed of *Potamogeton crispus*.

The estimated number of primary (mature) eggs was 3,167 (N = 1; 280 mm TL). Egg diameter (n = 50) ranged from 1.40 to 2.15 mm ($\bar{X}$ = 1.79 mm). The estimated time for egg development was 8 to 12 days.

The GSI reached a maximum in late February (male 0.34 percent and female 4.31 percent). This marked increase in the ratio between gonad weight and body weight in winter (February) was interpreted as the onset of the reproductive season. The GSI declined abruptly following spawning.

The following phases of the study will be completed in 1994-95: seasonal histology of the gonads, meristics (count) and morphometric measurement for sexual dimorphism, sex ratio, and laboratory spawning.

10 Natural History and Ecology of Anurans[1]

Introduction

There are 12 species of frogs and 3 species of toads in West Virginia (Table 59) (Green and Pauley 1987). Few studies have been conducted on the ecology and natural history of most species of anurans in the state. It was the purpose of the GBWMA anuran (frogs and toads) study (1) to determine what species were present, times of emergence from hibernation, and mating of all species, and (2) to determine ecological factors and interactions between *Rana pipiens* (northern leopard frog) and *Rana palustris* (pickerel frog). The latter objective was the major thrust of this study because GBWMA is one of the few known sites in North America where these two species are sympatric.

Taxonomy and description of the major study species

Kingdom Animalia
Phylum Chordata
Subphylum Vertebrata
Superclass Tetrapoda
Class Amphibia
Subclass Lissamphibia
Order Anura
Family Ranidae

Genus Rana L. Frogs in this genus are typically medium to large in size and have smooth skin and long legs with webbing between the toes. The rear margin of the tongue has a pair of lobelike projections. Members of this genus often have a glandular fold or ridge along each side of the back called dorsolateral folds (Green and Pauley 1987).

[1] Thomas K. Pauley, Ph.D; James W. Barron

Table 59
Anurans Found in West Virginia

Family	Scientific Name	Common Name
Pelobatidae	*Schaphiobus h. holbrooki*	Eastern Spadefoot
Bufonidae	*Bufo a. americanus*	Eastern American Toad
	Bufo woodhousii fowleri	Fowler's Toad
Hylidae	*Acris crepitans blanchardi*	Blanchard's Cricket Frog
	Acris c. crepitans	Northern Cricket Frog
	Hyla chrysoscelis	Gray Treefrog Complex
	Hyla versicolor	Gray Treefrog Complex
	Pseudacris brachyphona	Mountain Chorus Frog
	Pseudacris c. crucifer	Northern Spring Peeper
	Pseudacris triseriata feriarum	Upland Chorus Frog
Ranidae	*Rana catesbeiana*	Bullfrog
	Rana clamitans melanota	Green Frog
	Rana palustris	Pickerel Frog
	Rana pipiens	Northern Leopard Frog
	Rana sylvatica	Wood Frog

***Rana pipiens* Schreber**. *Rana pipiens* is a medium-sized ranid that may reach a head-body length of 5.1 to 10.2 cm. The dorsum is brown or green. The dorsolateral folds are lighter in color and extend from the eye to the groin. There are two or three rows of rounded spots with light colored borders between the dorsolateral folds. The ventral surface (belly and hind legs) is white (Green and Pauley 1987).

***Rana palustris* LeConte**. *Rana palustris* is a medium-sized ranid that reaches a snout-vent length of 7.6 cm. The back is brown or tan, and the dorsolateral folds are lighter and extend to the groin. Two rows of squarish spots lie between the dorsolateral folds. The undersides of the hind legs are bright yellow or orange (Green and Pauley 1987).

Objectives of study

One of the major objectives of this study was to determine and compare emergence and calling period (i.e., breeding period) for *Rana palustris* and *Rana pipiens* in the existing swamp and the created swamp. These areas will be referred to as the old swamp and the new swamp, respectively. To establish manageable study sites which included *R. pipiens* and *R. palustris*,

relatively large sections of the old swamp and new swamp were visited regularly until both species were found together. The site chosen in the old swamp was located behind the Jenkins House; the new swamp site was behind the barn (Figure 39). The old swamp site was significantly larger, and *R. palustris* and *R. pipiens* were abundant and harder to catch here. Differences in ease of capture were probably the result of vegetative differences between the sites. Superficially, the old swamp site was dominated by dense grasses and rushes west of the submerged farm road and buttonbush (*Cephalanthus occidentalis*) and other woody plants east of the road. The new swamp site was dominated by less dense grasses and rushes. A thorough vegetative analysis of the two study sites will be conducted in 1995.

Another objective of the study was to determine the emergence and calling period (i.e. breeding period) for all anurans at GBWMA. Emergence was determined by the first visual or auditory (i.e., call) account for each species. In addition, road surveys were done on four occasions during or shortly after rain. State Route 2 adjacent to GBWMA was driven once, and all amphibian species dead or alive were noted. Massive migrations of amphibians occur on this section of highway on rainy spring nights.

Methods and Materials

Data collection

On most visits, either one or both sites were thoroughly walked through. Environmental data including air temperature, water temperature, and relative humidity were taken at the arrival and departure of each visit. Also, all anurans species seen or heard during the visit were noted. Each time a *Rana pipiens* or *Rana palustris* was found or collected, the following parameters were measured: air temperature, water temperature, relative humidity, water pH, and three water depths at the perch. A distinct numbered flag was then placed at the perch to help locate the site.

Air temperature and relative humidity were measured at chest level. Water temperature and pH were measured at approximately 3 to 6 in. below the water surface. Air and water temperature were measured with a Reotemp soil thermometer to the nearest 0.5 °C. Relative humidity was measured to the nearest 1.0 percent with a Bacharach sling psychrometer. Water pH was measured with an Accumet 1003 portable pH meter to the nearest 0.1 of a unit. Water depth was measured to the nearest 0.5 cm.

Other data collected for each frog included snout-to-urostyle length, depth of frog in the water, and type of perch. Snout-to-urostyle length was measured to the nearest 0.05 mm with a dial Vernier caliper. The depth the frog was in the water was measured to the nearest 0.5 cm. Also noted was the type of vegetation the frog was perched on as well as whether it was calling, gravid, or in amplexus.

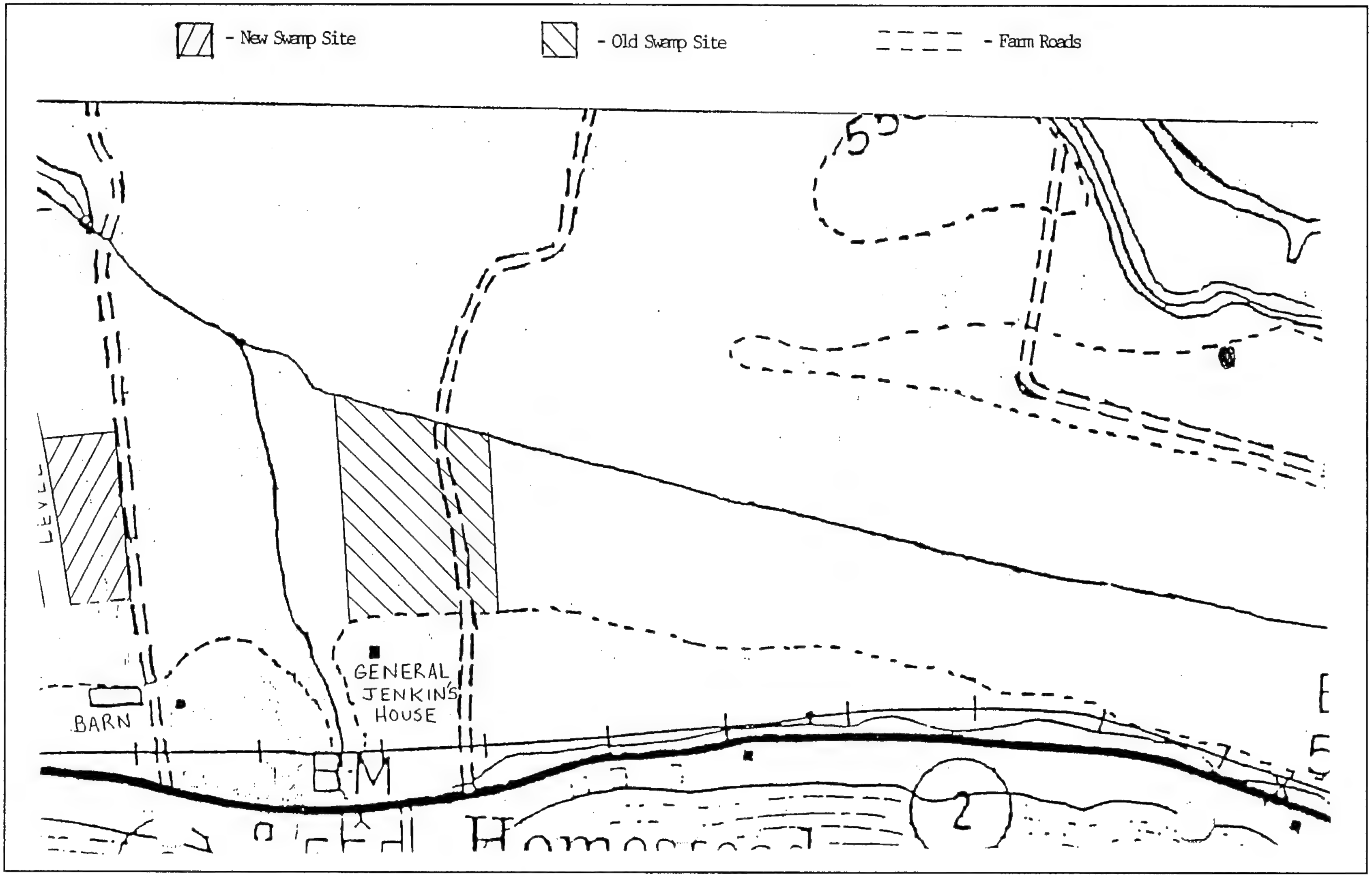


Figure 39. Close-up map of the new and old swamp sites at GBWMA

Each time an egg mass was observed, it was marked with a distinctly numbered flag. On 9 April the following data were collected for each mass: water depth (± 0.5 cm), egg mass depth (± 0.5 cm), and determination of what the mass was attached to. Eight egg masses were taken to the laboratory where the length, width, and height (± 0.1 mm) were measured with dial Vernier calipers. The outer envelope of five eggs from each of the eight masses was measured with dial Vernier calipers (± 0.01 mm). The number of eggs in the mass was estimated by 1) counting the number of eggs (usually 100 to 200) in a small portion of the mass, 2) placing the portion in a 1-L graduated cylinder with 300 ml of water, 3) measuring the water displacement of the portion with a 10 ml serological pipet (± 0.1 ml), 4) placing the whole mass in the graduated cylinder and measuring the water displacement as above, and 5) calculating an estimated number of eggs for the whole mass using the proportion of eggs per milliliter displaced by the portion.

Since environmental data were not collected for the egg masses, the data collected for the frogs during the laying period were used. The median water temperature, air temperature, and relative humidity and the mean pH for each visit were determined. These were then averaged for the laying period.

Statistical analysis

Statistical tests were made by using a one-way ANOVA with Newman-Keuls multiple comparisons ($\alpha = 0.05$).

Results

This report includes data collected from May 1993 through May 1994. Eight species of anurans were observed in GBWMA (Tables 60 and 61). Five of the eight species emerged in February, and the remaining three emerged in March or May. Three species, *Rana sylvatica* (wood frog), *R. pipiens*, and *Pseudacris c. crucifer* (northern spring peeper), are early breeders that typically deposit eggs in February and March. *Bufo a. americus* (eastern American toad) and *R. palustris* typically breed in March and April, while *R. clamitans melanota*, *R. catesbeiana*, and *Hyla chrysocelis* breed from April through June and July. Of the eight species observed in GBWMA, six were found in the old swamp (Table 60), and eight were found in the new swamp.

Water temperature, air temperature, relative humidity, water pH, and water depth in the new and old sections of the swamp were compared. There were no significant differences between the new and old swamp for either water temperature or air temperature ($p < 0.05$) (Figure 40). The new section of the swamp had significantly higher pH values than the older section ($p < 0.05$) (Figure 40). There were no significant differences in water depth or relative humidity between the two sections of the swamp ($p < 0.05$) (Figure 41).

Table 60
Dates of Emergence and Calling Males for all Species of Anurans Observed in the Old Swamp

Species	Emergence	Calling
P. c. crucifer	2/21/94	2/21/94 - 5/6/94[1]
R. catesbeiana	2/24/94	4/18/94 - 5/6/94[1]
R. c. melanota	2/21/94	4/18/94 - 5/6/94[1]
R. palustris	3/21/94	4/2/94 - 5/6/94[1]
R. pipiens	2/21/94	3/7/94 - 4/10/94
R. sylvatica	2/21/94	2/21/94 - 3/7/94

[1] This was the last date the site was visited before this report.

Table 61
Dates of Emergence and Calling Males for all Species of Anurans Observed in the New Swamp

Species	Emergence	Calling
B. a. americanus	3/7/94	3/23/94 - 4/23/94
H. chrysoscelis	5/7/94	5/7/94[1]
P. c. crucifer	2/18/94	2/18/94 - 5/7/94[1]
R. catesbeiana	3/4/94	4/9/94 - 5/7/94[1]
R. c. melanota	5/1/94	5/1/94 - 5/7/94[1]
R. palustris	3/7/94	4/5/94 - 5/7/94[1]
R. pipiens	2/19/94	3/4/94 - 4/9/94
R. sylvatica	3/4/94	3/4/94 - 3/12/94

[1] This was the last date the site was visited before this report.

Natural history data for the two major study species, *R. pipiens* and *R. palustris*, showed that *R. pipiens* emerged from hibernation on 21 February in the old swamp and on 19 February in the new swamp. Calling for *R. pipiens* occurred from 7 March to 10 April in the old swamp and from 4 March to 9 April in the new swamp. *Rana palustris* emerged on 21 March in the old swamp and on 7 March in the new swamp. They called from 2 April to mid May in the old swamp and from 5 April to mid May in the new swamp (Tables 60 and 61).

Areas of the swamp that were used as breeding sites by *R. pipiens* and *R. palustris* were studied in detail. Since both species are relatively explosive

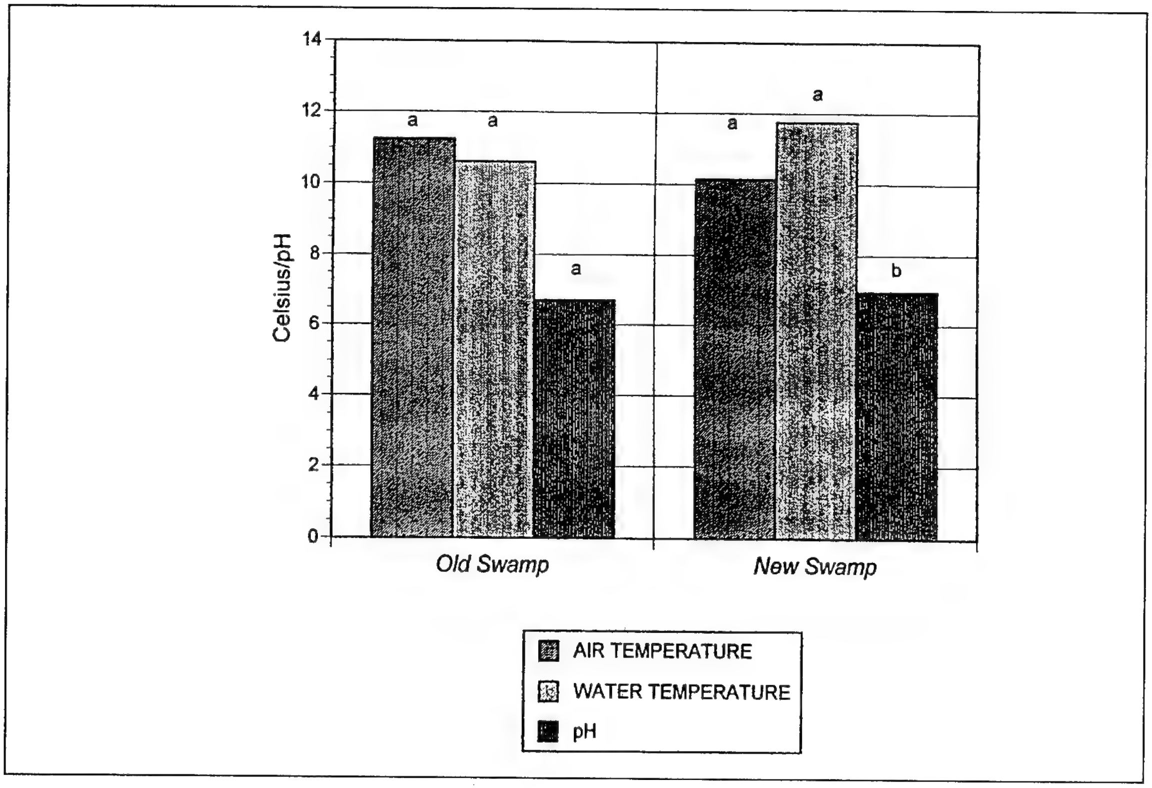


Figure 40. Mean water temperature, air temperature, and water pH for old swamp versus new swamp

breeders and mate within 2 weeks of each other, it was necessary to concentrate on the ecology and natural history of *R. pipiens* during 1994. More detailed studies on *R. palustris* will be conducted in 1995. Parameters measured for both species in their respective breeding habitats included water temperature, air temperature, relative humidity, water pH, and water depth. Water depth was compared for males, females, and immatures for both species. In addition, water depth at perch sites was compared for mature males of both species. General vegetation types were also examined at perch sites.

No significant differences were found for water temperature, air temperature, and water pH between the two species ($p < 0.05$) (Figure 42). There was no significant difference in relative humidity between the two species ($p < 0.05$) (Figure 43). However, *Rana pipiens* was found in significantly deeper water than *R. palustris* ($p < 0.05$) (Figure 43).

Mean water depths were compared for the two species in areas of the old and new sections of the swamp. There was no significant difference in water depths used by *R. palustris* between the two sections of the swamp, but *R. pipiens* was found in significantly deeper water in the new section ($p < 0.05$) (Figure 44). Water depth at the perch for mature males was compared between species at each site. When mature males from both sites were compared, there was no significant difference in water depth between species.

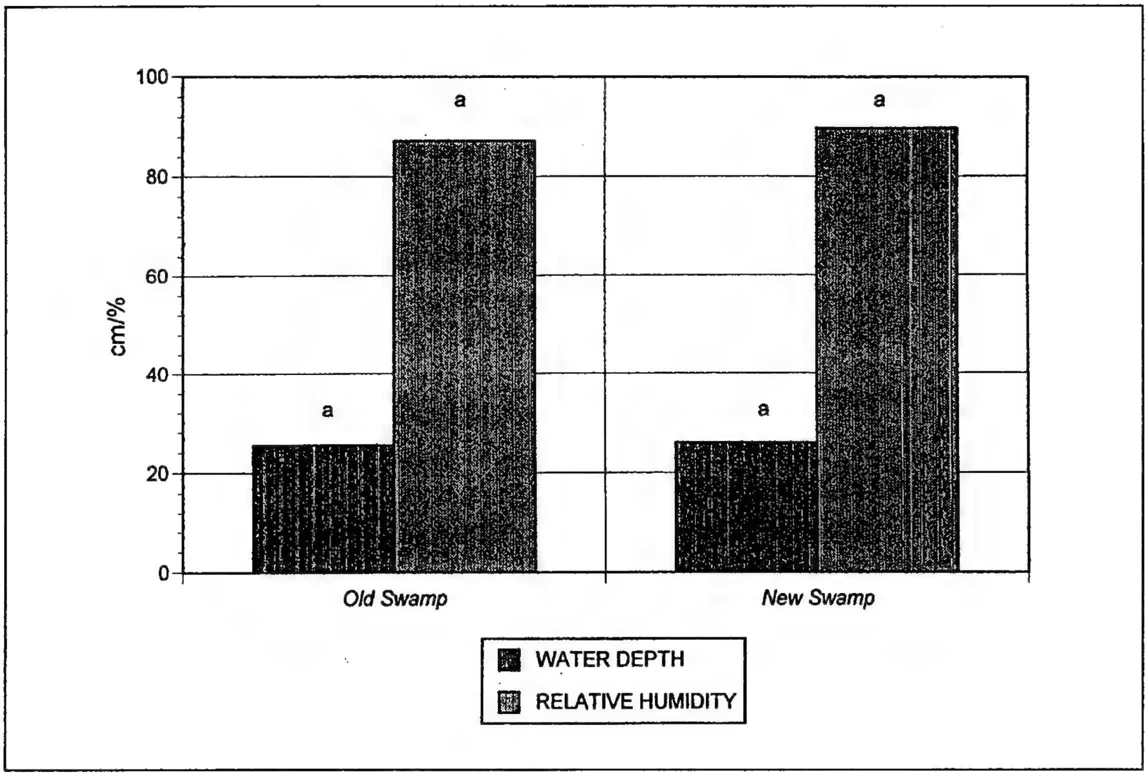


Figure 41. Mean water depth and relative humidity for old swamp versus new swamp

In the new swamp there was no significant difference in water depth for mature male *R. palustris* and *R. pipiens*. However, mature male *R. palustris* were in significantly deeper water in the old swamp site ($p < 0.05$) (Table 62).

Perch types were compared for *R. palustris* and *R. pipiens*. Data presented in Table 61 show that 76 percent of all *R. pipiens* observed in the new swamp were found in the grassy areas in the middle, while only 20 percent of all *R. palustris* observed were in the grassy sections in the middle (Table 63). Perch types were also compared between *R. palustris* males, *R. pipiens* males, felmales, and immatures. Seventy percent of male *R. palustris* were found on grass on the bank of the levee. Conversely, 80 percent of male *R. pipiens* were found in the grass in the middle of the swamp. Sixty-three percent of the female and 100 percent of the immature *R. pipiens* were found in the grass in the middle (Table 63).

Time of egg deposition for *R. pipiens* was from 5 March through 9 April. During this time, 39 egg masses were studied and the following data collected: air temperature, water temperature, pH, relative humidity, and morphological characteristics of the egg masses. Thirty-three of the 39 egg masses were deposited from 20 March to 27 March. Therefore, the environmental data from this period were compared to the 5 March to 19 March period and the 28 March to 9 April period. A total of only six masses was deposited during both of these periods. No significant differences were found between the

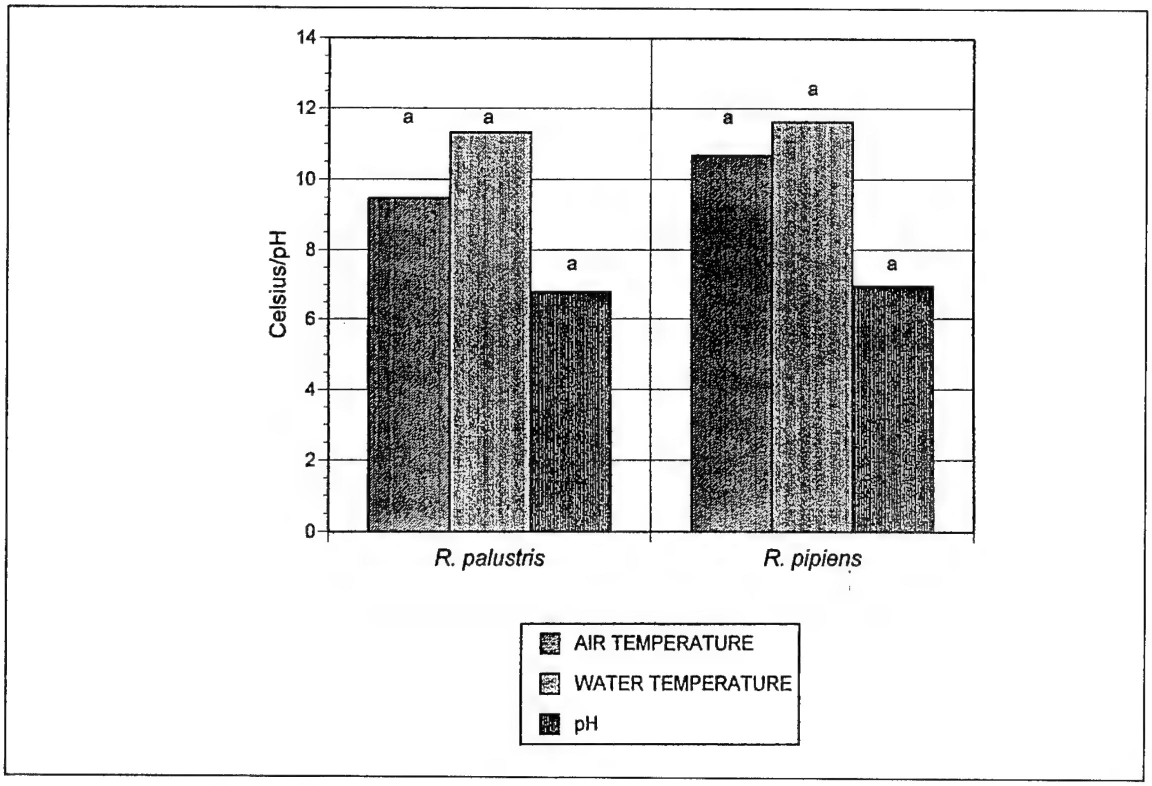


Figure 42. Mean water temperature, air temperature, and water pH for *R. palustris* versus *R. pipiens*

environmental parameters (Table 64). However, when the last period was grouped with the middle period, significant differences between air and water temperatures were evident. The earlier period from 5 March to 19 March was significantly cooler ($P<0.05$) (Table 64).

The mean length of *R. pipiens* egg masses was 77.5 mm, mean width was 59.1 mm, and mean height was 39.7 mm. The mean diameter per egg was 4.3 mm; the estimated number of eggs per mass was 1,937 (Table 65). In addition, it was found that 86 percent of all *R. pipiens* egg masses were attached to grass, 11 percent to rushes, and 3 percent to woody plants (Table 66).

Discussion

Eight species of frogs and toads have been found to breed in GBWMA. This represents one of the largest aggregations of breeding anurans known to occur in West Virginia. In addition to the largest number of species found to breed in the area, this study concurred with emergence data and first date for calling for each of the 8 species (Green and Pauley 1987). Exceptions are the date that *R. catesbeiana* and *R. c. melanota* first start to call. Green and

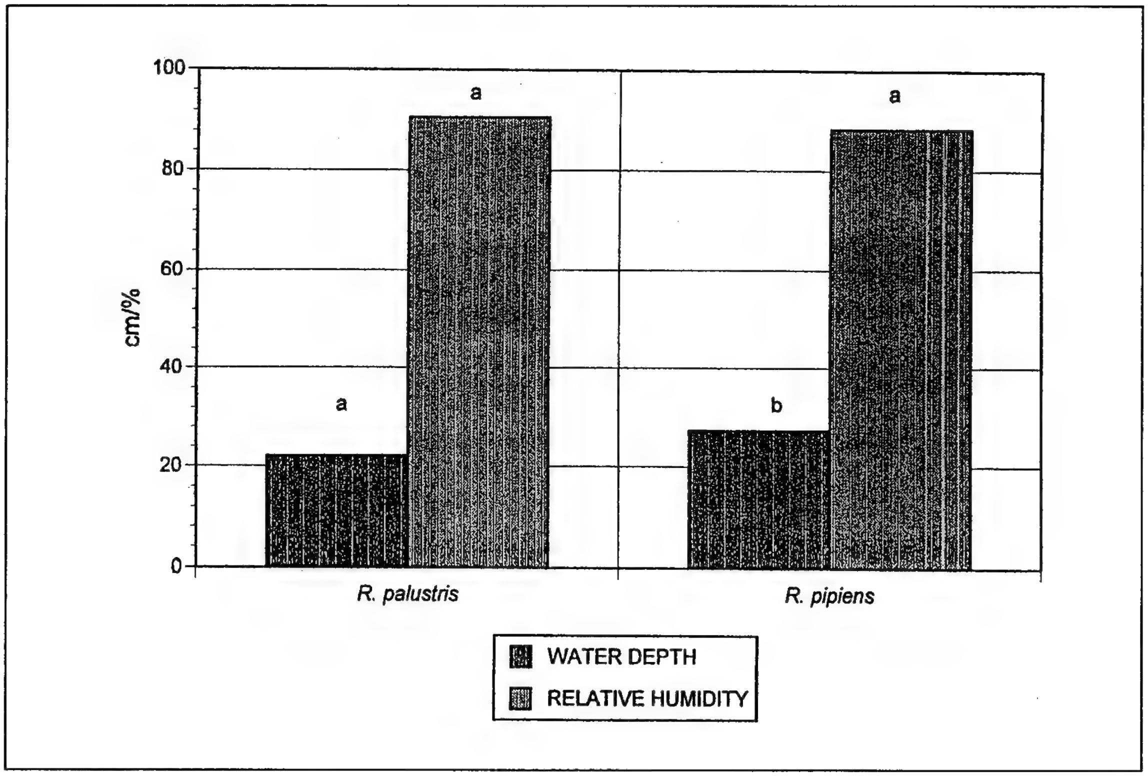


Figure 43. Mean water depth and relative humidity for *R. palustris* versus *R. pipiens*

Pauley (1987) reported that *R. catesbeiana* starts calling in mid May; *R. c. melanota* starts calling in late April. In this study, *R. catesbeiana* started calling in early April, and *R. c. melanota* calls in mid April.

The new swamp was created in 1992 as part of a mitigation and waterfowl enhancement program by the WVDNR. The development of new wetlands provided an opportunity to determine the success of amphibians in created wetlands and compare the use of created wetlands with established wetlands. This study showed that all species found to breed in the old swamp are successfully breeding in the new swamp. In addition, two species not yet found in the old swamp (*H. chrysoscelis* and *B. a. americanus*) are using the new swamp as a breeding habitat.

With the exception of pH, environmental parameters where the anurans breed were found to be the same in the new and old sections of the swamp. Although significant, the difference in pH is not a concern since all values were close to being neutral (7.0). The significance of these data supports the development of new wetlands for amphibian breeding habitats.

Some of the major objectives for the first year of this study were to determine overlap in breeding times, habitat selection, and habitat partitioning between the two species. *Rana pipiens* emerges from hibernation in mid February, starts calling in early March, and mates/deposits eggs in mid March;

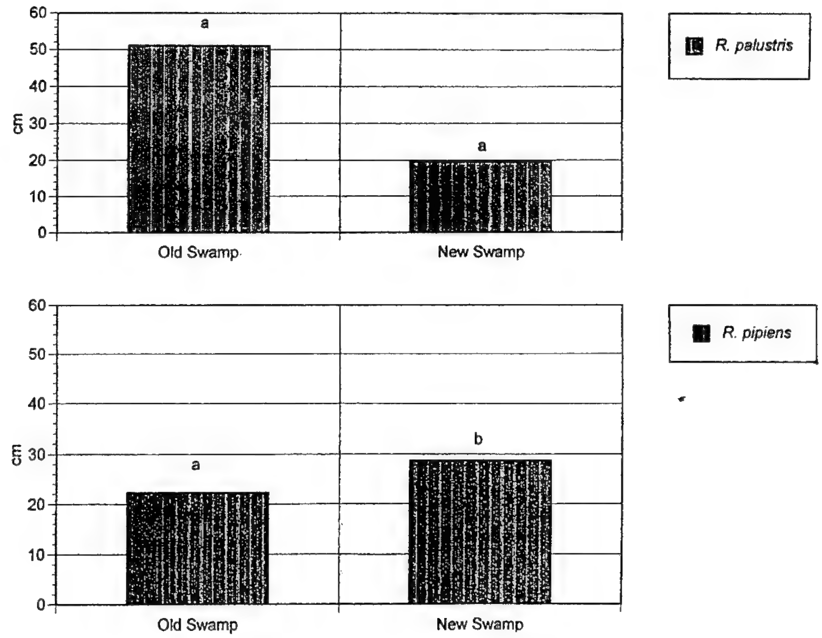


Figure 44. Mean water depth for *R. palustris* and *R. pipiens* at old swamp and new swamp sites

Table 62
Mean Water Depth (cm) at Perch for Mature Male *R. palustris* Versus Mature Male *R. pipiens*

Mature Males[1] Old and New Swamp		Mature Males[1] Old Swamp		Mature Males[1] New Swamp	
R. palustris	*R. pipiens*	*R. palustris*	*R. pipiens*	*R. palustris*	*R. pipiens*
$34.92^{a} \pm 15.28$ (n = 5)	$28.89^{a} \pm 7.49$ (n = 41)	$51.05^{a} \pm 4.60$ (n = 2)	$22.03^{b} \pm 5.91$ (n = 6)	$24.17^{a} \pm 4.79$ (n = 3)	$30.07^{a} \pm 7.15$ (n = 35)

Note: Between species, mean values with different superscripts were found to be siginificantly different ($p < 0.05$).
[1] Mature males in this case include all calling males and sexually mature males caught when conspecifics were calling.

R. palustris emerges in mid to late March and starts calling in early April. There is a 9-day overlap in the time that the two species start calling in the new swamp and a 5-day overlap in the old swamp. Most of the egg deposition for *R. pipiens* was completed by 27 March (36 of 39 egg masses found in new swamp were laid by 27 March). This is 9 days before *R. palustris* started

Table 63
Perch Types for *Rana palustris* and *Rana pipiens*

Species	Bottom Vegetation	Grass in Middle	Rush	Grass on Submerged Levee Bank	Algal Mat	Button Bush	Vegetation	None
Rana palustris	--	4	1	14	--	1	--	--
Rana pipiens	2	54	3	7	1	--	3	1
Rana palustris males	--	4	1	14	--	1	--	--
Rana pipiens males	1	36	2	2	1	--	3	--
Rana pipiens females	1	12	1	5	--	--	--	--
Rana pipiens immatures	--	3	--	--	--	--	--	--

Table 64
Environmental Data for Different Periods of Egg Laying in the New Swamp Site

Egg Laying Period	Number of Masses Found	Air Temperature °C	Water Temperature °C	Relative Humidity, %	pH
03/05/94 to 03/19/94	3	$5.16^a \pm 3.05$ (n = 7)	$8.10^a \pm 2.24$ (n = 6)	$96.0^a \pm 5.7$ (n = 2)	$7.0^a \pm 0.3$ (n = 3)
03/20/94 to 03/27/94	33	$10.40^a \pm 3.38$ (n = 4)	$12.37^a \pm 2.77$ (n = 3)	--	$7.1^a \pm 0.3$ (n = 2)
03/28/94 to 04/09/94	3	$10.60^a \pm 5.82$ (n = 3)	$12.33^a \pm 2.52$ (n = 3)	$85.5^a \pm 20.5$ (n = 2)	$7.0^a \pm 0.0$ (n = 2)
03/05/94 to 03/19/94	3	$5.16^a \pm 3.05$ (n = 7)	$8.10^a \pm 2.24$ (n = 6)	$96.0^a \pm 5.7$ (n = 2)	$7.0^a \pm 0.3$ (n = 3)
03/20/94 to 04/09/94	36	$10.49^b \pm 4.13$ (n = 7)	$12.35^b \pm 2.40$ (n = 6)	$85.5^a \pm 20.5$ (n = 2)	$7.1^a \pm 0.2$ (n = 5)

Note: Mean values with different superscripts were found to be significantly different ($p < 0.05$).

Table 65
Egg Characteristics for *Rana pipiens* at the New Swamp Site

Characteristics	N	Mean	Standard Deviation	Minimum	Maximum
Length of Mass (mm)	8	77.55	15.17	46.50	95.50
Width of Mass (mm)	8	59.15	9.29	42.50	69.00
Height of Mass (mm)	8	39.70	8.62	24.00	50.30
Egg Diameter[1] (mm)	5[2]	4.35	0.48	3.74	4.84
Estimated Number of Eggs	8	1,937	300.5	1,611	2,560

[1] Diameter of the outer envelope of one egg.
[2] Each N value is equal to the average of five egg diameters from one mass.

Table 66
Vegetation to Which *Rana pipiens* Egg Masses Were Attached

	Grass	Rush	Shrub/Woody Plant
Number of Masses	33[1]	4	1

[1] Eighty-six percent of the masses were attached to grass.

calling. Calling (breeding) dates of these two sympatric species at GBWMA are separated by nearly 2 weeks. While this disparity of calling (breeding) times probably serves as a reproductive isolating mechanism at GBWMA, this is not to say that interbreeding could not occur in a year with a late, short spring and an early summer. Additional studies would be necessary to determine whether this could occur.

Evidence was found in this study that suggests that these species do not breed in the same habitat. In the old swamp, *R. palustris* occupies much deeper water. In the new swamp, there was no significant difference in the water depth of the two species. The new swamp does not have the deeper, open water habitat found in the old swamp. *Rana pipiens* was most frequently found in the grassy areas near the middle of the new swamp. This is comparable to the habitat where it was found to breed in the old swamp. Without deep, open water in the new swamp, *R. palustris* moved to the submerged bank of the levee, which supported much less emergent vegetation. It seems that habitat selection/partitioning exists between these two species.

Detailed studies of the reproductive characteristics of *R. pipiens* revealed the following data. In the study site of the new swamp, 39 egg masses were found. Three masses were found between 5 March and 19 March, 33 between 22 to 27 March, and 3 masses between 28 March and 9 April. In addition, 62 egg masses were found in the new swamp outside the study site. Twenty-two of these were in a 1- to 2-m^2 area and 40 more masses in a second 1- to

2-m^2 area. Ten egg masses in the study site were also found in a 1- to 2-m^2 area. The congregation of egg masses in 1- to 2-m^2 areas agrees with observations by Wright and Wright (1949).

Air and water temperature proved to be important regulating factors for egg deposition. As described above, eggs in the study site were deposited in three periods of time: 5 to 19 March, 22 to 27 March, and 28 March to 9 April. Thirty-six (85 percent) were deposited from 22 March to 9 April. Air and water temperatures were significantly warmer during these dates than in early March. It appears, therefore, that temperature is the major environmental factor that regulates egg deposition in *R. pipiens*.

Rana pipiens was found to call and deposit eggs in shallow water with grasses in both sections of the swamp, while *R. palustris* called in deeper water with woody plants in the old swamp. Thirty-three (86 percent) of *Rana pipiens* masses studied were attached to grasses and only 1 (3 percent) was attached to woody plants. These data clearly demonstrate that habitat selection is an important factor in segregating the gene pools of these two species (Table 66).

Wright and Wright (1949) reported the egg mass of *R. pipiens* is 75 to 150 mm by 5 to 75 mm and individual eggs 3 to 5 mm. Egg masses at GBWMA were somewhat smaller averaging 77.5 mm by 59.1 mm. Zenisek (1963) reported 300 to 800 eggs per mass. At GBWMA, egg masses averaged 1,937 eggs per mass. Individual eggs averaged 4.3 mm.

Summary and Conclusions

To date, this study has revealed that eight species of toads and frogs breed in GBWMA. Emergence times and mating times were established for each of these species; and it was found that *R. catesbeiana* and *R. c. melanota* call earlier than previously reported. Two species, *R. pipiens* and *R. palustris*, were studied in detail, and the following information was obtained: *Rana pipiens* emerges from hibernation in mid February and calls from early March to early April; *Rana palustris* emerges from hibernation in early to mid March and calls from early April to mid May; *Rana pipiens* deposits eggs from early March to early April. Egg masses contain an average of 1,937 eggs attached to grasses, and egg deposition was correlated with air and water temperature. *Rana pipiens* called and deposited eggs in shallow, grassy areas while *R. palustris* called in deeper water with woody shrubs.

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Appendix A
Vegetation and Land Use Maps

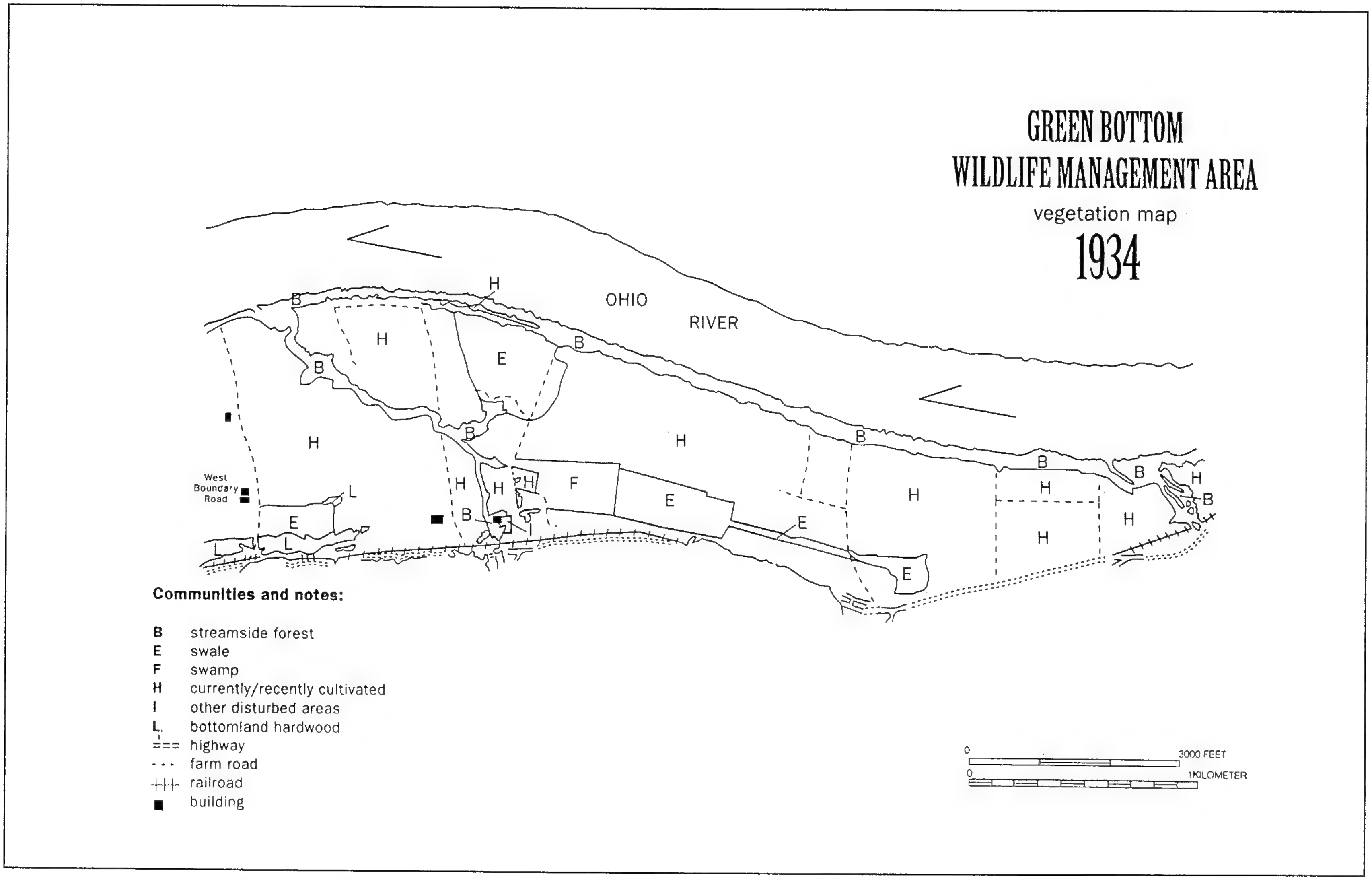


Figure A1. Vegetation and land use map drawn from a 1934 aerial photograph of GBWMA

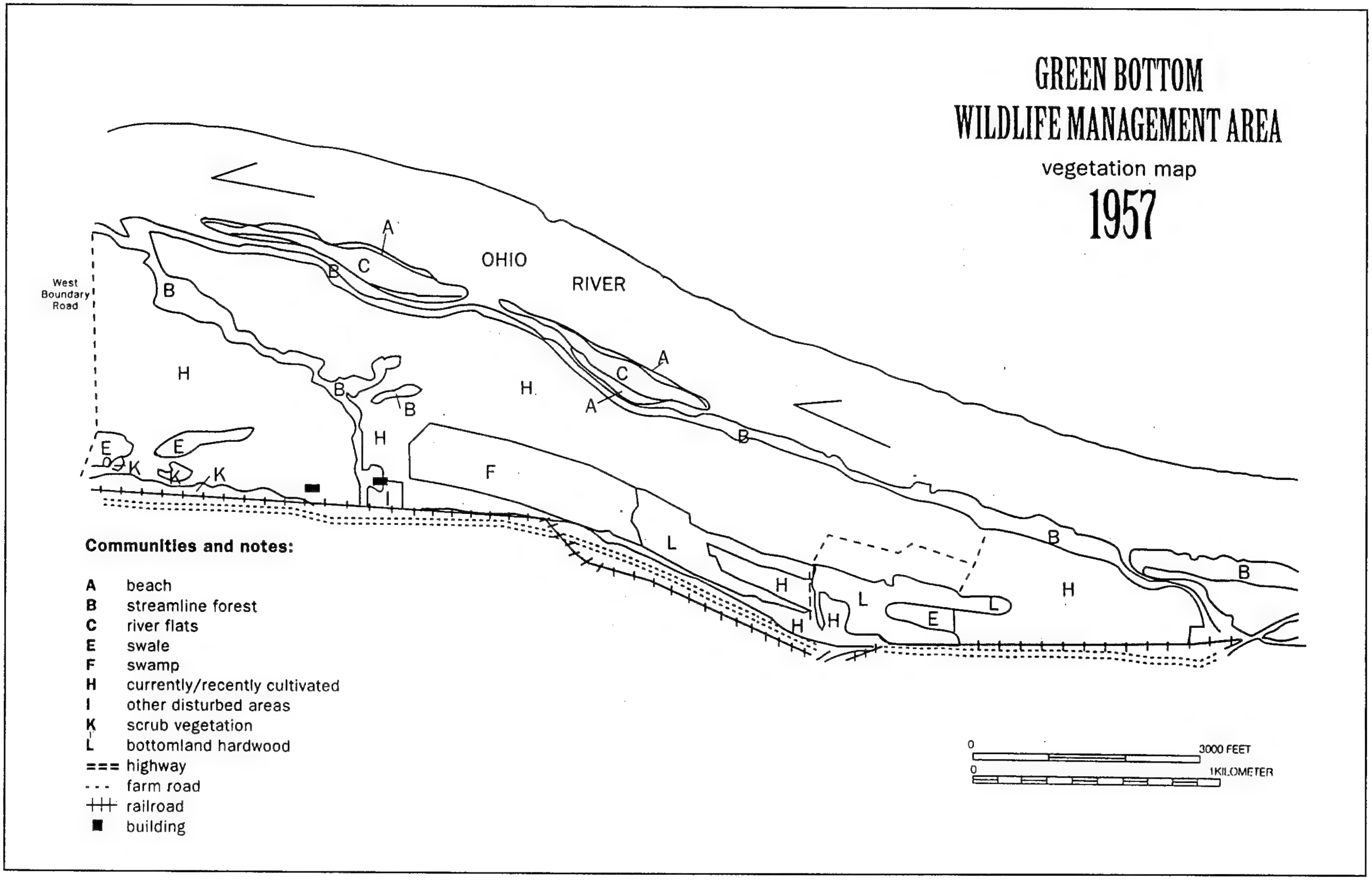


Figure A2. Vegetation and land use map drawn from a 1957 aerial photograph of GBWMA

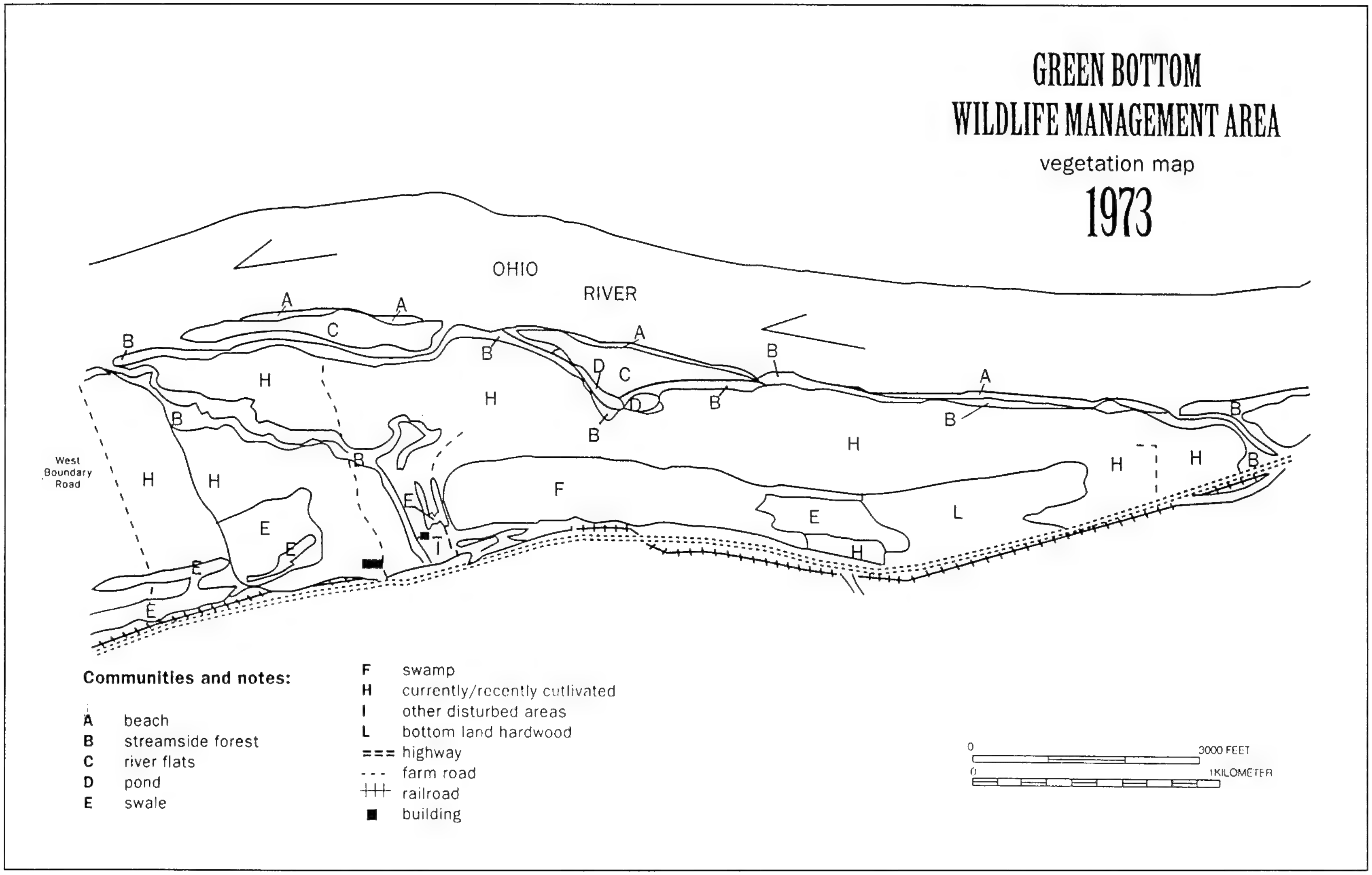


Figure A3. Vegetation and land use map drawn from a 1973 aerial photograph of GBWMA

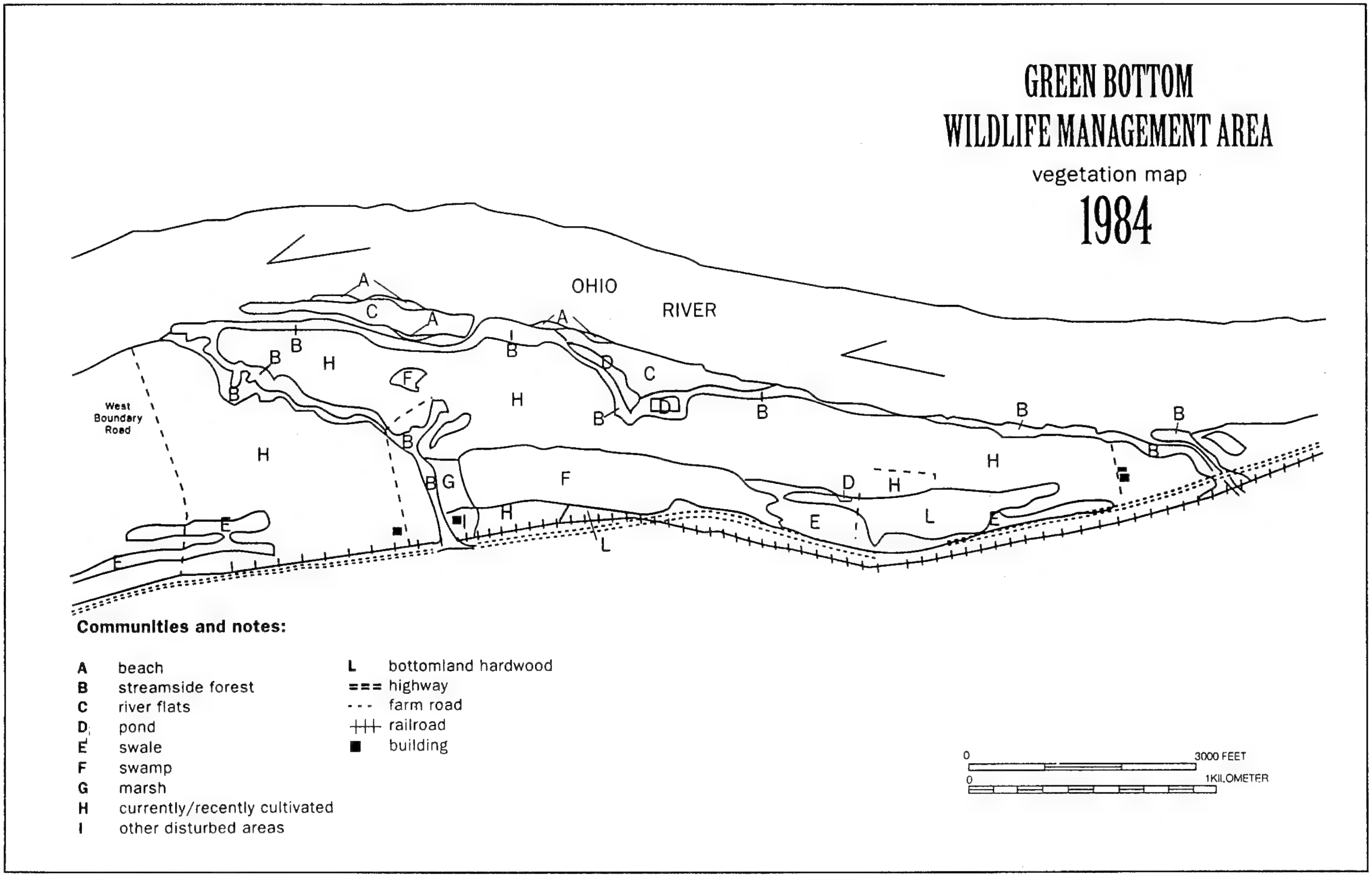


Figure A4. Vegetation and land use map drawn from a 1984 aerial photograph of GBWMA

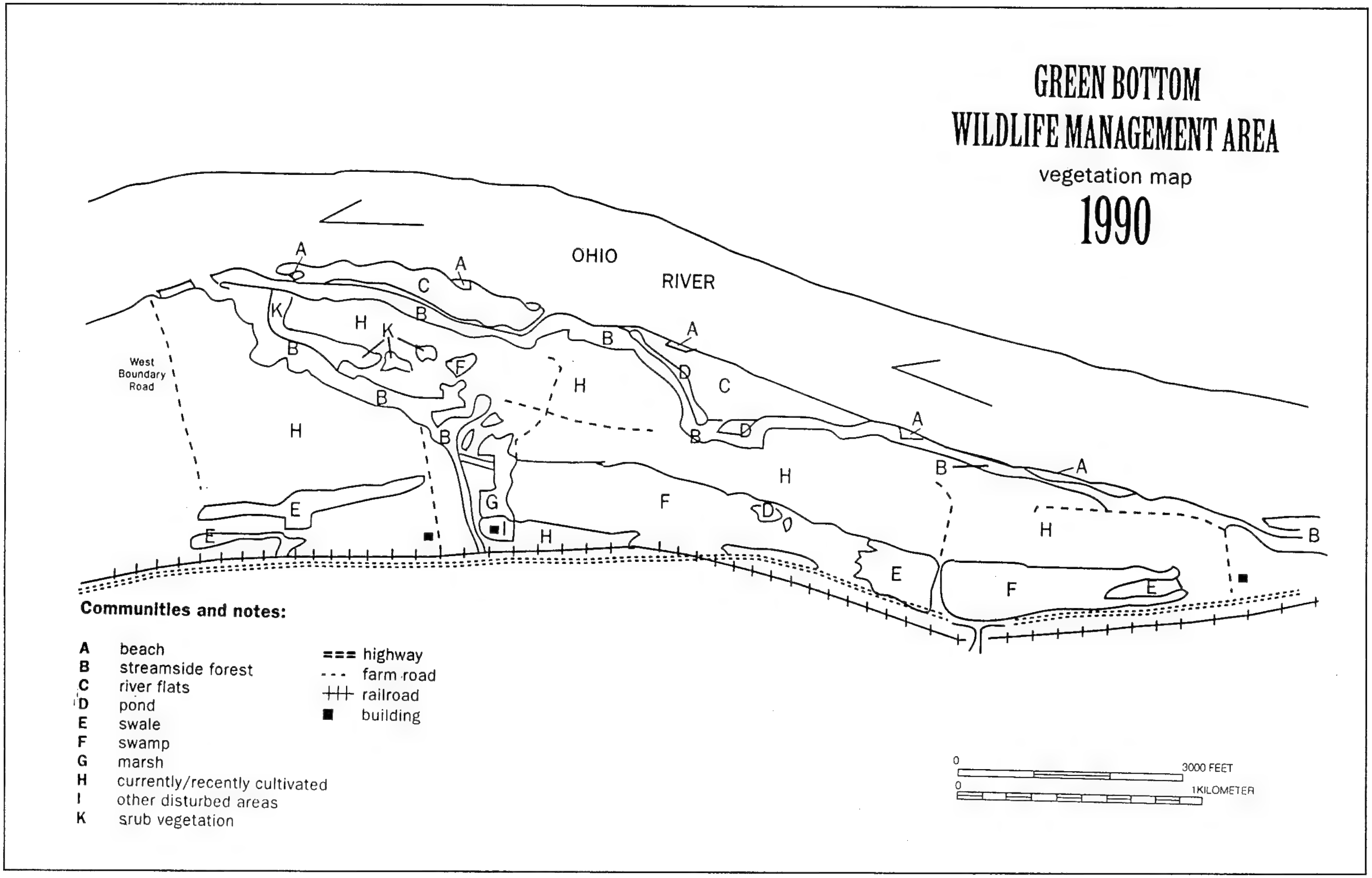


Figure A5. Vegetation and land use map drawn from a 1990 aerial photograph of GBWMA

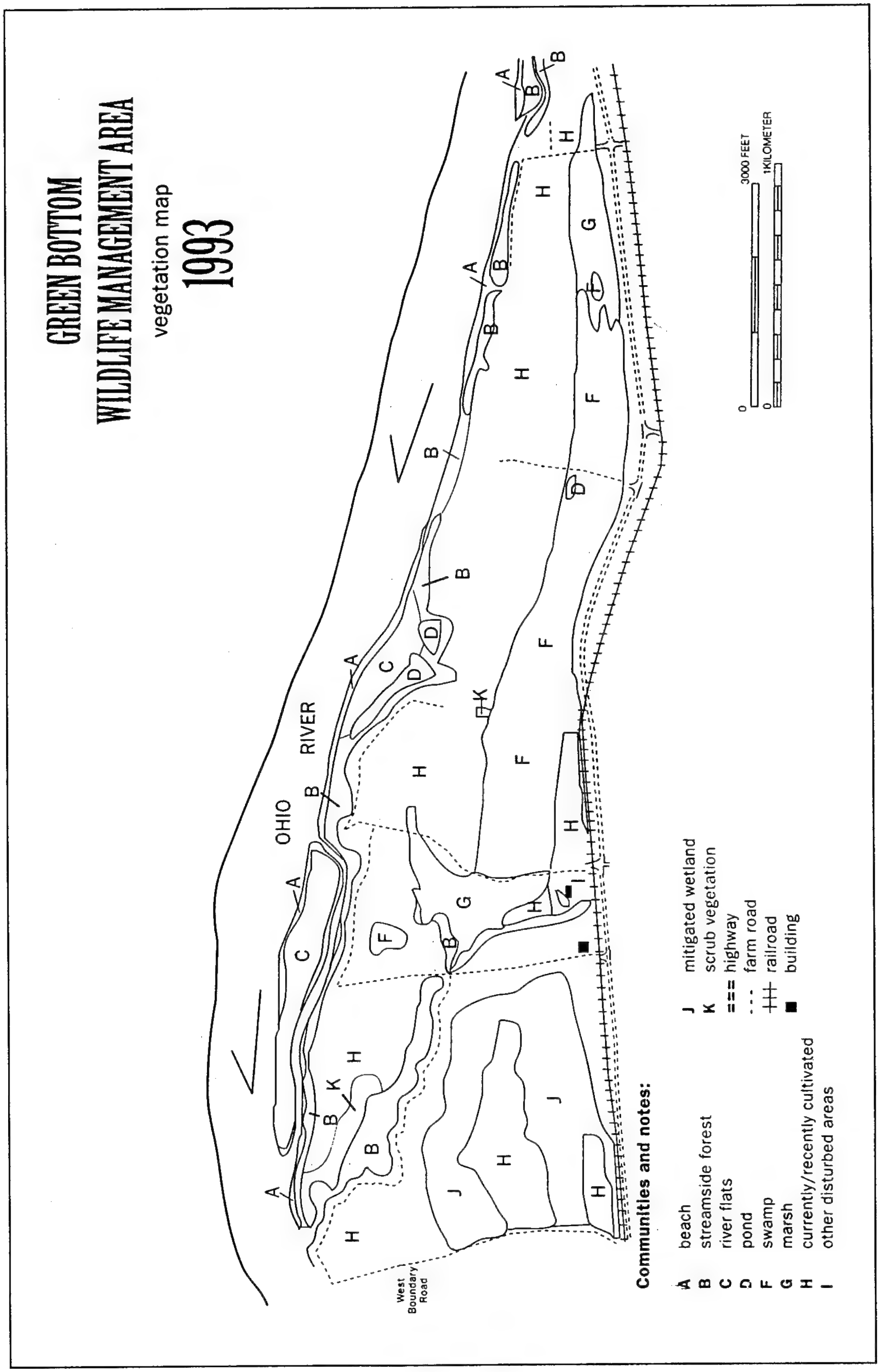
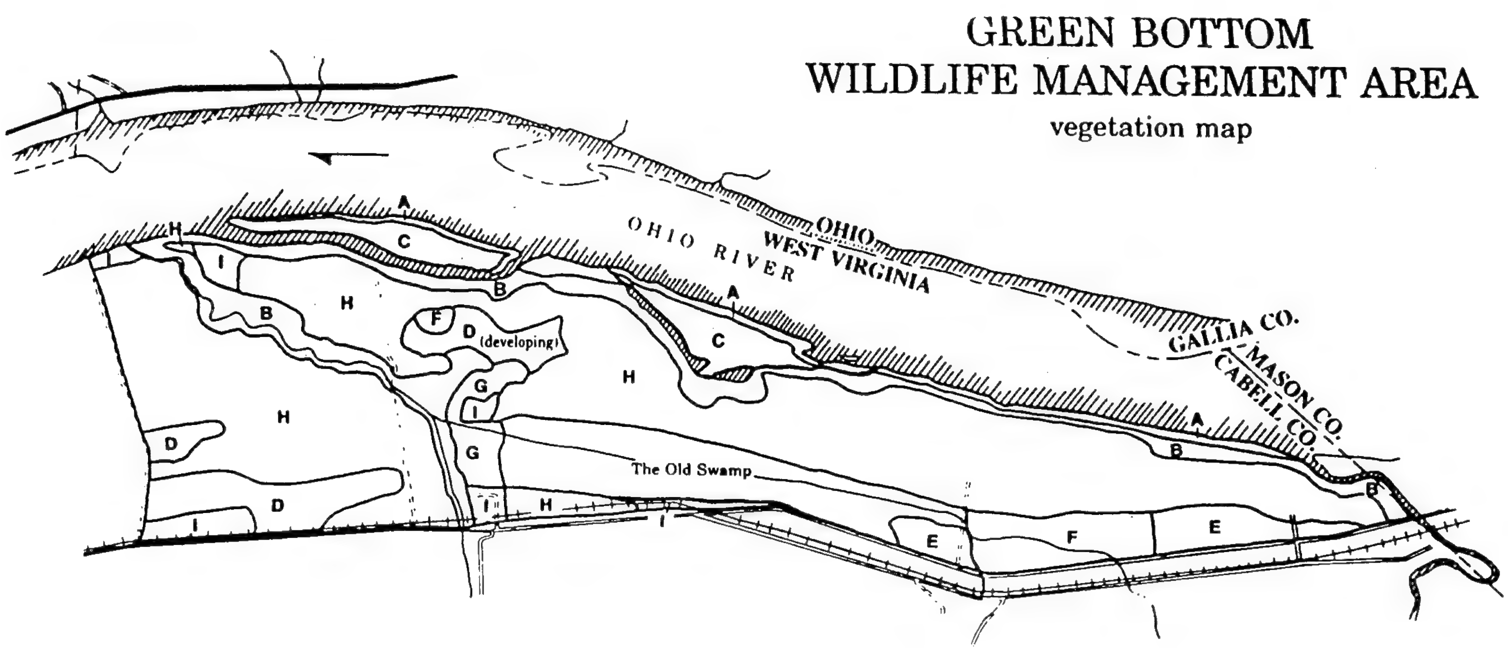


Figure A6. Vegetation and land use map drawn from 1993 mitigation planning maps of GBWMA

Appendix B
Map of the Plant Communities at GBWMA



Communities and notes:

A	beach	**E**	old swale	**I**	other disturbed areas
B	streamside forest	**F**	swamp		
C	river flats	**G**	marsh		
D	new swale	**H**	currently/recently cultivated		

Figure B1. Map of the plant communities at GBWMA

Appendix C
Map of Landmarks for Use in Locating Floristic Elements

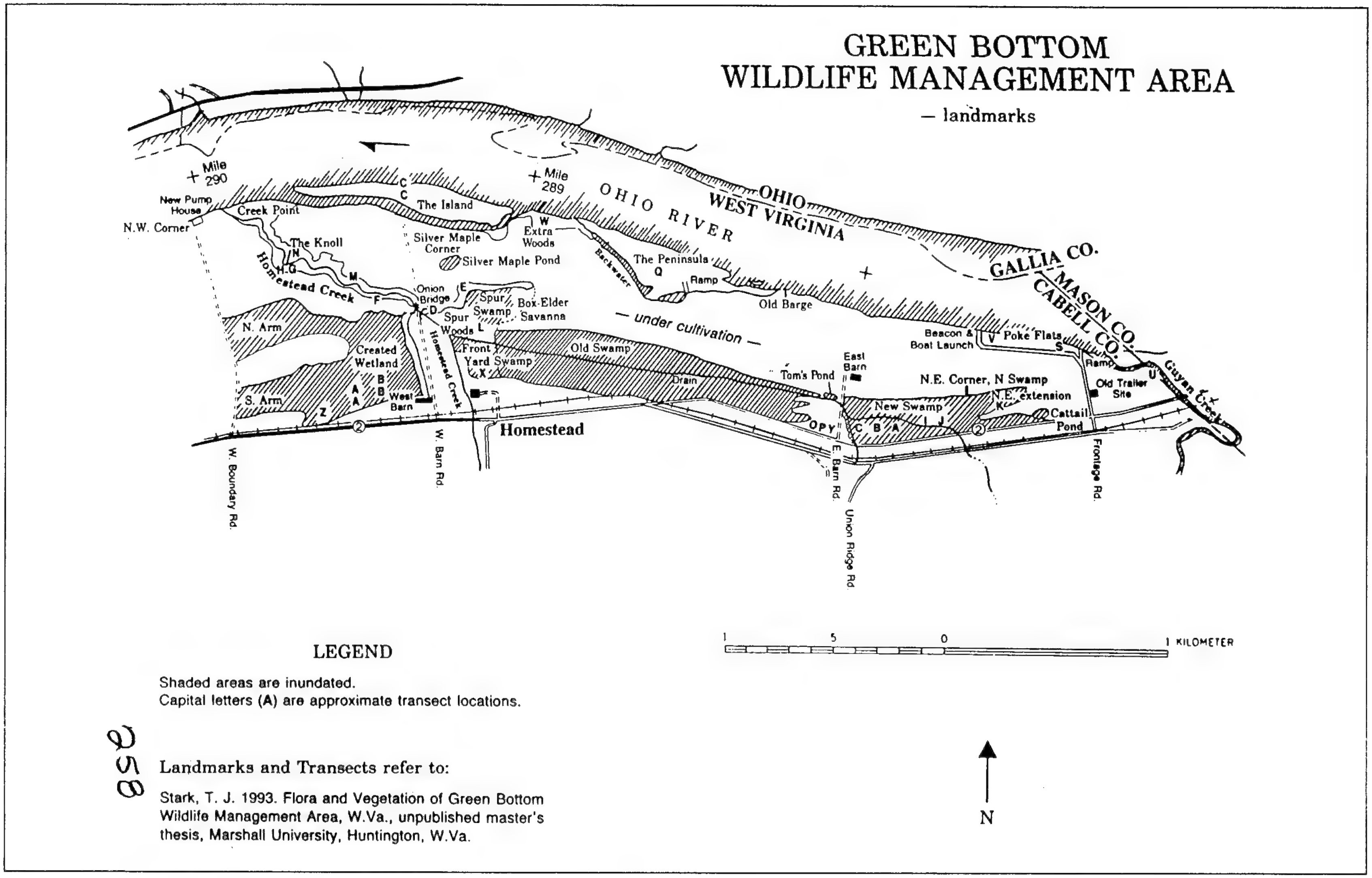


Figure C1. Map of landmarks for use in locating floristic elements

Appendix D
Eight-Letter Species Codes for All Taxa in Data Tables

Eight Letter Codes

ACAL RHO *Acalypha rhomboidea*

ACER NED *Acer negundo dead*

ACER NEG *Acer negundo*

ACER RUB *Acer rubrum*

ACER SAC *Acer saccharinum*

ACER SAD *Acer saccharinum dead*

AGAL TEN *Agalinis tenuifolia*

AGRO CAP *Agrostis capillaris*

AGRO PER *Agrostis perennans*

AGRO SPP *Agrostis species*

ALIS SUB *Alisma subcordatum*

ALNU SER *Alnus serrulata*

AMAR SPP *Amaranthus species*

AMBR ART *Ambrosia artimisiifolia*

AMOR FRU *Amorpha fruticosa*

AMPE COR *Ampelopsis cordata*

AMPH BRA *Amphicarpaea bracteata*

ANAX JUN *Anax junius*

APIO AME *Apios americana*

APOC CAN *Apocynus cannabinum*

ARCT MIN *Arctium sinus*

ARIS DRA *Arisaema dracontium*

ARTE VUL *Artemesia vulgaria*

ARTH HIS *Arthraxon hispidus*

ARUN GIG *Arundinaria gigantea*

ASAR CAN *Asarum canadense*

ASCL INC *Asclepias incarnata*

ASTE DUM *Aster dumosus*

ASTE LAT *Aster lateriflorus*

ASTE SPP *Aster species*

BIDE DIS *Bidens discoidea*

BIDE FRO *Bidens frondosa*

BIDE POL *Bidens polylepis*

BIDE SPP *Bidens species*

BIDE TRI *Bidens tripartita*

BOEH CYL *Boehmeria cylindrica*

BROM JAP *Bromus japonicus*

CALY SEP *Calystegia sepium*

CAMP RAD *Campsis radicans*

CARE AMP *Carex amphibola*

CARE CRI *Carex crinita*

CARE CRI *Carex cristatella*

CARE FRA *Carex frankii*

CARE GRA *Carex grayii*

CARE JAM *Carex jamesii*

CARE LUP *Carex lupulina*

CARE LUR *Carex lurida*

CARE PRO *Carex projecta*

CARE SPP *Carex species*

CARE STI *Carex stipata*

CARE TRI *Carex tribuloides*

CARE VUL *Carex vulpinoidea*

CARY COR *Carya cordiformis*

CARY LAC *Carya laciniosa*

CARY SPP *Carya species*

CELT OCC *Celtis occidentalis*

CEPH OCC *Cephalanthus occidentalis*

CHEN AMB *Chenopodium ambrosioides*

CHEN BER *Chenopodium berlandieri*

CINN ARU *Cinna arundinacea*

CIRS ARV *Cirsium arvense*

CIRS VUL *Cirsium vulgare*

COMM COM *Commelina communis*

CORN AMO *Cornus amomum*

CORO VAR *Coronilla varia*

CRYP CAN *Cryptotaeneia canadensis*

CUPH VIS *Cuphea viscosissima*

CUSC GRO *Cuscuta gronovii*

CYNA LAE *Cynanchum laeve*

CYPE ODE *Cyperus oderatus*

CYPE SPP *Cyperus species*

CYPE STR *Cyperus strigosus*

DESM CAN *Desmodium canescens*

DIGI ISC *Digitaria ischaesus*

DIGI SAN *Digitaria sanguinalis*

DIOD VIR *Diodia virginica*

DIPS SYL *Dipsacus sylvestria*

ECHI CRU *Echinochloa crusgalli*

ECLI PRO *Eclipta prostrate*

ELEO OVA *Eleocharis ovata*

ELEU IND *Eleusine indica*

ELYM VIR *Elymus virginicus*

EPIL COL *Epilobium coloratum*

EQUI ARV *Equisetum arvense*

ERAG PEC *Eragrostia pectinacea*

EREC HIE *Erectites hieracifolia*

ERIG PHI *Erigeron philadelphicus*

ERIG SPP *Enigeron species*

ERYT SIM *Erythemis simplicicollis*

EUPA COE *Eupatorium coelestinum*

EUPA FIS *Eupatorium fistulosum*

EUPA PER *Eupatorium perfoliatum*

EUPA SER *Eupatorium serotinum*

EUPH HUM *Euphorbia humistrata*

EUTH GRA *Euthamia grasinifolia*

FEST ELA *Festuca elatior*

FEST OBT *Festuca obtusa*

FRAX AMD *Fraxinus americana deed*

FRAX AME *Fraxinus americana*

FRAX PED *Fraxinus pennsylvanica deed*

FRAX PEN *Fraxinus pennsylvanica*

GALI APA *Galium aparine*

GALI TIN *Galium tinctorium*

GEUM CAN *Geum canadense*

GEUM LAC *Geum laciniatum*

GEUM SPP *Geum species*

GLEC HED *Glechoma hederacea*

GLED TRI *Gleditsia triancanthos*

GLYC STR *Glyceria striata*

HIBI MOS *Hibhiscus moscheutos*

HUMU LUP *Humulus lupulus*

HYPE MUT *Hypericum mutilum*

YPE PUN *Hypericum punctatum*

IMPA CAP *Impatiens capensis*

IMPA PAL *Impatiens pallida*

IPOM PAN *Ipomoea pandurata*

JUGL NID *Juglans nigra deed*

JUGL NIG *Juglans nigra*

JUNC EFF *Juncus effusus*

JUNC SPP *Juncus species*

JUNC TEN *Juncus tenuis*

JUST AME *Justicia americana*

LAPO CAN *Laportea canadensis*

LEER ORY *Leersia oryzoides*

LEER VIR *Leersia virginica*

LEMN MIN *Lemna minor*

LIBE CYA *Libellula cyanea*

LIBE LUC *Libellula luctuosa*

LIBE PUL *Libellula pulchella*

LIBE SEM *Libellula semifusciata*

LIND BEN *Lindera benzoin*

LIND DUB *Lindernia dubia*

LONI JAP *Lonicera japonica*

LONI MOR *Lonicera morrowi*

LUDW ALT *Ludwigia alternifolia*

LUDW PAL *Ludwigia pelustria*

LYCO AME *Lycopus americanus*

LYCO COM *Lycopus uniflorus/ virginicus*

LYSI NUM *Lysimachia nummularia*

LYSI TER *Lysimachia terrestris*

MELI SPP *Melilotus species*

MENI CAN *Menispermum canadense*

MENT ARV *Mentha arvensis*

MICR VIN *Microstegium vimineum*

MIMU RIN *Mimulus ringens*

MOLL VER *Mollugo verticillata*

NYSS SYL *Myssa sylvatica*

OENO SPP *Oenothera species*

ONOC SEN *Onociea sensibilis*

OXAL STR *Oxalis stricta*

PACH LON *Pachydiplax longipennis*

PANI CLA *Panicum clandestinum*

PANI VIR *Panicum virgatum*

PART QUI *Parthenocissus quinquefolia*

PASP LAE *Paspalum laeve*

PENT SED *Penthorum sedoides*

PHAR ARU *Phalaris arundinacea*

PHYT AME *Phytolacca americana*

PILE PUM *PIlea pumila*

PLAN RUG *Plantago rugelii*

PLAT LYD *Plathemis lydia*

PLAT OCC *Platanus occidentalis*

PLAT OCD *Platanus occidentalis dead*

POA SPP *Poa species*

POA TRI *Poa trivialis*

POLI ACR *Polystichum acrostichoides*

POLY CES *Polygonum cespitosum*

POLY COC *Polygonum coccineum*

POLY CUS *Polygonum cuspidatum*

POLY HYD *Polygonum hydropiperoides*

POLY PEN *Polygonum pensylvanicum*

POLY SAG *Polygonum sagittatum*

POLY VIR *Polgonum virginianus*

POPU DED *Populus detoides dead*

POPU DEL *Populus deltoides*

POTA CRI *Potamogeton crispus*

PRUN SED *Prunus serotina dead*

PRUN SER *Prunus setotina*

PRUN VUL *Prunella vulgaris*

PYRU SPP *Pyrus species*

ROBI PSD *Robinia pseudo-acacia dead*

ROBI PSE *Robinia pseudo-acacia*

RORI PAL *Rorippa palustria*

ROSA MUL *Rosa multiflora*

ROTA RAM *Rotala ramosior*

RUBU SPP *Rubus species*

RUDB LAC *Rudbeckia laciniata*

RUME VER *Rumex verticillatus*

SAGI LAT *Sagittaria latifolis*

SALI EXI *Salix exiqua*

SALI NID *Salix nigra dead*

SALI NIG *Salix nigra*

SAMB CAN *Sambucus canadensis*

SAUR CER *Saururus Cernuus*

SCIR ATR *Scirpus atrovirens*

SCIR CYP *Scirpus cyperinus*

SCUT LAT *Scutellaria laterifolis*

SENE AUR *Senecio aureas*

SETA GLA *Setaria glauca*

SICY ANG *Sicyos angulatus*

SIDA HER *Sida hermaphrodita*

SMIL HIS *Smilax hispida*

SMIL RAC *Smilacina racemosa*

SOLA CAR *Solanum carlinense*

SOLA NIG *Solanum nigrum*

SOLI CAN *Solidago canadensis*

SOLI GIG *Solidago gigantea*

SOLI SPP *Solidago species*

SPAR EUR *Sparganium eurycarpum*

SPIR POL *Spirodela polyrhiza*

STAC HIS *Stachys hispida*

STRO HEL *Strophostyles helvola*

SYMP VIC *Sympetrum vicinum*

TARA OFF *Taraxacum officinale*

THAL PUB *Tahlictrum pubescens*

TILI AMD *Tilia americana dead*

TILI AME *Tilia americana*

TOXI RAD *Toxicodendron radicans*

TRAM LAC *Tramea loceruta*

TYPH LAT *Typha latifolia*

ULMU AMD *Ulmus americana dead*

ULMU AME *Ulmus americana*

ULMU SPP *Ulmus species*

URTI DIO *Urtica dioica*

VERB ALT *Verbesina alternifolia*

VERB HAS *Verbena hastata*

VERN GIG *Vernonia gigantea*

VIOL SOR *Viola sororia*

VITI RIP *Vitis riparia*

WOLF COM *Wolffia columbiana/ papulifers*

XANT STR *Xanthium strumarium*

Appendix E
Raw Data for Pre-inundation Period Soils at GBWMA

Table E1
Raw Data for Pre-inundation Period Soils at GBWMA

Site	Depth	Redox	Sand	Clay	Silt	pH	Ca	K	Mg	P	Cu	Fe	Mn	Zn	NO_3	NH_4	CEC	OM
msa1	10	413.4	11.4	27.7	60.9	5.3	1,292	145	231	3.0	1.73	12	20	10.5	8.8	3.6	9.4	7.5
msa1	20	446.0	5.9	29.2	64.9	5.5	1,235	74	201	2.1	1.85	14	15	8.3	2.6	3.4	8.4	6.5
msb1	10	386.7	18.3	25.6	56.1	5.7	1,399	138	252	2.9	1.49	11	26	10.8	4.5	6.7	9.4	7.5
msb1	20	411.2	10.7	28.1	61.2	5.7	1,395	78	224	2.0	2.10	11	17	8.3	1.2	3.4	9.0	7.0
msa2	10	375.8	32.7	12.6	54.7	5.7	1,575	112	255	3.9	2.75	39	45	11.9	5.5	4.8	10.4	9.5
msa2	20	347.8	19.5	25.8	54.6	5.9	1,640	86	274	2.7	2.32	19	23	8.3	6.2	3.0	10.6	7.5
msb2	10	256.6	22.2	26.9	50.9	6.1	1,876	112	301	3.9	1.74	18	37	9.9	11.0	4.4	12.1	9.5
msb2	20	150.1	17.5	28.9	53.6	6.1	1,667	110	280	3.0	2.91	16	28	8.5	6.0	3.8	10.9	8.0
msa3	10	177.2	35.7	12.5	51.8	5.7	1,672	153	270	3.7	2.50	27	40	13.5	6.9	4.2	11.1	10.0
msa3	20	245.0	22.0	25.4	52.5	5.9	1,714	75	252	2.7	3.10	18	25	11.0	5.8	3.6	10.8	8.5
msb3	10	33.8	36.8	12.4	50.8	5.5	1,575	102	239	4.2	3.14	65	47	13.5	3.8	5.1	10.6	9.5
msb3	20	95.5	34.7	14.0	51.3	5.7	1,584	72	234	2.6	2.36	25	28	11.1	5.4	3.0	10.0	8.0
ysa1	10	-292.4	12.2	37.4	50.4	5.1	1,010	150	145	6.2	2.93	251	123	5.4	0.5	73.5	7.8	6.5
ysb1	10	-304.6	4.8	35.2	60.0	5.2	917	150	145	5.7	2.39	226	172	4.2	0.5	75.0	7.1	5.5
osa1	10	-138.4	8.9	33.2	57.9	5.3	784	123	115	5.4	1.98	248	222	3.5	0.5	58.0	5.9	5.0
osa1	20	-166.6	4.9	37.7	57.5	5.6	892	102	132	5.4	1.87	214	301	1.7	0.6	50.0	5.9	5.0
osb1	10	-173.9	8.6	37.3	54.1	5.1	754	113	108	7.3	2.91	297	108	7.4	1.1	63.5	6.1	6.5
osb1	20	-187.0	6.6	36.7	56.7	5.2	856	92	131	4.3	3.92	199	138	4.1	0.8	40.5	6.4	5.0

Note: Units for all variables are those used in tables. Sites beginning with "ms" are old-field plots; those beginning with "ys" are young swamp plots; and those beginning with "os" are old swamp plots. Replicate plots are designated "a" and "b". Old-field transects are "1" at the highest elevation and "2" and "3" at lower elevations.

Appendix F
Raw Data for Post-inundation Period Soils at GBWMA

Table F1
Raw Data for Post-inundation Period Soils at GBWMA

Site	Depth	Redox	Sand	Clay	Silt	pH	Ca	K	Mg	P	Cu	Fe	Mn	Zn	NO^3	NH_4	CEC	OM
msa1	10	-58.3	11.6	25.1	63.3	5.3	1,262	142	226	3.9	0.8	16	23	11.8	1.0	2.5	9.5	10.5
msa1	20	10.2	15.2	30.6	54.2	5.5	1,238	100	200	2.4	1.1	14	14	9.3	1.2	1.9	8.6	9.4
msb1	10	24.5	21.6	23.6	54.8	5.9	1,557	147	300	3.4	0.9	9	18	9.6	0.6	2.5	10.6	11.1
msb1	20	2.4	13.3	32.2	54.5	5.8	1,407	87	236	2.2	1.1	12	12	8.2	0.7	1.6	9.2	9.4
msa2	10	-262.3	23.4	24.9	51.7	5.7	1,394	127	230	2.2	1.4	85	14	8.9	2.3	74.1	9.3	13.9
msa2	20	-282.0	21.5	26.1	52.5	5.9	1,509	88	262	1.9	1.3	17	4	7.1	6.9	26.5	9.9	13.4
msb2	10	-284.9	21.3	21.4	57.3	5.8	1,503	121	243	2.5	1.4	77	29	8.4	2.0	64.7	9.8	12.7
msb2	20	-287.4	24.1	22.1	53.8	6.0	1,711	94	274	2.8	1.5	35	43	8.4	6.7	18.6	11.0	11.5
msa3	10	-276.1	27.7	22.9	49.4	5.4	1,163	134	174	4.0	1.9	201	79	14.0	0.3	93.2	8.4	13.6
msa3	20	-286.2	19.9	30.8	49.3	5.9	1,634	96	258	2.8	1.6	48	52	9.3	6.1	28.7	10.5	12.1
msb3	10	-298.7	16.8	29.5	53.7	5.8	1,563	89	255	3.3	1.8	83	61	9.7	2.6	18.9	10.2	11.8
msb3	20	-322.6	17.2	29.5	53.3	6.0	1,603	73	265	2.8	1.6	44	46	9.0	3.4	9.3	10.3	11.8
ysa1	10	-320.9	5.7	41.0	53.4	5.0	813	118	126	3.1	2.4	139	277	5.0	0.2	64.8	6.8	9.2
ysa1	20	-326.6	5.7	41.0	53.4	5.6	1,021	99	175	2.6	1.0	84	424	1.2	0.2	43.5	7.1	8.0
ysb1	10	-326.0	6.5	37.6	56.0	5.2	876	146	124	2.8	1.4	138	224	4.9	0.1	57.4	6.8	11.0
ysb1	20	-332.7	6.5	37.6	56.0	5.5	947	118	155	2.7	1.2	103	274	2.6	0.5	45.4	6.8	9.4
osa1	10	-333.6	9.3	38.1	52.6	5.1	803	114	119	5.2	1.6	236	129	5.7	0.1	63.5	6.5	8.3
osa1	20	-345.6	9.7	36.2	54.1	5.2	903	96	143	3.9	1.8	144	140	4.4	0.5	33.2	7.0	7.7
osb1	10	-325.7	9.3	39.3	54.4	5.1	771	100	113	4.2	1.9	191	127	9.0	0.1	64.1	6.3	9.9
osb1	20	-328.7	5.1	41.2	53.7	5.3	895	84	146	2.2	1.5	81	110	4.6	0.6	32.4	6.7	9.7

Note: Units for all variables are those used in tables. Sites beginning with "ms" are old-field plots; those begining with "ys" are young swamp plots; and those beginning with "os" are old swamp plots. Replicate plots are designated "a" and "b". Old-field transects are "1" at the highest elevation and "2" and "3" at lower elevations.

REPORT DOCUMENTATION PAGE

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OMB No. 0704-0188

1. AGENCY USE ONLY *(Leave blank)*	2. REPORT DATE	3. REPORT TYPE AND DATES COVERED
	November 1995	Final report

4. TITLE AND SUBTITLE
Mitigated Wetland Restoration: Environmental Effects at Green Bottom Wildlife Management Area, West Virginia

5. FUNDING NUMBERS
WU 32761

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8. PERFORMING ORGANIZATION REPORT NUMBER

9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)
U.S. Army Corps of Engineers, Washington, DC 20314-1000;
U.S. Army Engineer Waterways Experiment Station
3909 Halls Ferry Road, Vicksburg, MS 39180-6199

10. SPONSORING/MONITORING AGENCY REPORT NUMBER
Technical Report
WRP-RE-10

11. SUPPLEMENTARY NOTES
Available from National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22161.

12a. DISTRIBUTION/AVAILABILITY STATEMENT
Approved for public release; distribution is unlimited.

12b. DISTRIBUTION CODE

13. ABSTRACT *(Maximum 200 words)*

Many of the nation's freshwater wetlands have been lost to land development. There is a critical need for restoration efforts to reclaim some of these wetlands. This study examines nine aspects of a restoration project and the project's effect on the environment.

1. Land use at the Green Bottom Wildlife Management Area (GBWMA) in the late 19th and 20th Centuries is analyzed. Wetlands are evaluated from a historical perspective from 1934 through 1994 in terms of diversity and size. Results indicate significant wetland destruction as farming intensity increased.

2. A comprehensive analysis of vascular plants and plant communities at GBWMA is undertaken. Results define seven vegetation types. These vegetation types are arranged along a moister gradient: steamside forest, river flats, beach, new swale, old swale, marsh, and swamp.

3. The physical and chemical parameters of the soil are examined. The examination includes changes in soil oxidation-reduction potential and texture, organic matter, pH, extractable macronutrients, and extractable micronutrients. Results indicate that mitigation wetland soils are developing toward true wetland soils following 8 months of inundation. However, mitigation soils lack some of the characteristics of hydromorphic soils, most notably are

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14. SUBJECT TERMS		15. NUMBER OF PAGES
Wetland mitigation	Wetland soil characteristics	229
Wetland restoration	Wetland animal communities	16. PRICE CODE
Wetland plant communities		

17. SECURITY CLASSIFICATION OF REPORT	18. SECURITY CLASSIFICATION OF THIS PAGE	19. SECURITY CLASSIFICATION OF ABSTRACT	20. LIMITATION OF ABSTRACT
UNCLASSIFIED	UNCLASSIFIED		

13. (Concluded).

extractable Mn and P and higher organic matter. Therefore, it is concluded that 8 months is an insufficient period of time for a complete change in these soils.

4. The practicality of establishing five woody species by direct planting of cuttings gathered from a nearby bottomland forest is assessed. The five species consist of 2 tree species, black willow (*Salix nigra*) and green ash (*Fraximus pennsylvanica* var. *subintegerrima*), and 3 shrub species, common alder (*Alnus serrulata*), buttonbush (*Cephalanthus occidentialis*), and silky dogwood (*Cornus amomum*). Results indicate that *C. occidentalis, C. amomum,* and *S. nigra* have a higher probability of success.

5. Nitrogen availability using *in situ* incubations of soils taken from three distinct habitat conditions based on degree of inundation during wetland creation is evaluated. Results indicate that available N exhibits a substantial shift following inundation of old-field soils from relatively equal amounts of NO_3 and NH_4 to a near predominance of NH_4. Also, extractable N is significantly greater following inundation of old-field soils because of the accumulation of NH_4.

6. The dynamics of 25 species of mosses and four species of liverworts in eight wetland communities located within the floodplain of the Ohio River are examined. Results indicate that the highest moss cover is from the families Amblystegiaceae and Brachytheciaceae. The liverwort with the greatest cover and largest number of species is from the family Ricciaceae.

7. Resident odonate populations within GBWMA prior to habitat modification are examined. The results provide a species list as well as information concerning territoriality, mating behavior, and cannibalism in naiadal adonates.

8. Reproductive activities of the local population of grass pickerel is examined. The results provide a baseline for managing the reproductive activities of the grass pickerel at GBWMA.

9. Comparisons of the emergence and calling (breeding) period are made for the northern leopard frog (*Rana pipiens*) and the pickerel frog (*Rana palustris*) in the existing swamp and the created swamp. Also of interest is determining the emergence and calling period of all anurans at GBWMA. Results indicate that *R. pipiens* emerges in mid February and calls from early March to early April; *R. palustis* emerges in early to mid March and calls from early April to mid May. Eight species of frogs and toads have been found to breed at GBWMA. This represents one of the largest aggregations of breeding anurans known to occur in West Virginia.

Documenting impacts of mitigation/restoration efforts on plant and animal communities is essential for increasing understanding of the ecological processes involved when natural or man-made changes occur in wetland and riparian communities. GBWMA is an important research, teaching, and recreational resource. The information gathered serves as a reference data bank for wetland restoration projects.